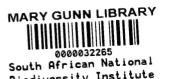


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JOURNAL OF SOUTH AFRICAN BOTANY

VOLUME 42

1976

Published under the authority
of the
Trustees
of the
National Botanic Gardens
of
South Africa,
Kirstenbosch,
Newlands, C.P.

Editor:

Prof. H. B. Rycroft

Director,
National Botanic Gardens
of
South Africa,
Harold Pearson
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of
Cape Town





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VOLUME 42

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Het by haar verpligtinge as voltydse universiteitsdosent wat verantwoordelik is vir die doseer van sitologie, biosistematiek, embriologie en anatomie, met toewyding navorsing gedoen. Sy het belangrike bydraes gemaak tot die sitologie van die Proteaceae en die Aizoaceae, die embriologie van die Haemodoraceae en die morfologie en taksonomie van Romulea, Syringodea en Homoglossum. Op grond van haar publikasies is die Havengaprys vir Biologie in 1974 deur die Suid-Afrikaanse Akademie vir Wetenskap en Kuns aan haar toegeken.

Sedert 1948 het daar dikwels artikels van haar, sewe daarvan in Afrikaans, in hierdie tydskrif verskyn. Haar belangrikste publikasie *The genus Romulea in South Africa* is in 1972 as Supplement 9 van hierdie tydskrif gepubliseer.



DIE KNOOP- EN BLAARSTEELMORFOLOGIE VAN DIE SUID-AFRIKAANSE VERTEENWOORDIGERS VAN DIE GENERA ADENOLO-BUS (HARV.) TORRE & HILLC., BAUHINIA L., PILIOSTIGMA HOCHST. EN TYLOSEMA (SCHWEINF.) TORRE & HILLC.*

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UITTREKSEL

Die stingels van die genera Adenolobus, Bauhinia, Piliostigma en Tylosema het deurgaans tipiese trilakunêre knope en die blare word afwisselend op die stingels gedra. Die laterale blaarspore vorm elk 'n tak wat die steunblare van vaatweefsel voorsien voordat hulle in die blaarsteel by die mediane blaarspoor aansluit.

Vir die doel van die bespreking, word die vaatweefsel in die blaarsteel in 'n aantal sones verdeel naamlik die eerste oorgangsone, pulvinêre sone, tweede oorgangsone, mediane sone,

derde oorgangsone en distale verdikking.

Die uitbeelding van die vaatweefsel in die blaarsteel is kenmerkend vir elke soort en die blaarspore ondergaan anastomosering en vertakking vanaf die pulvinus tot by die distale verdikking. In die distale verdikking verdeel die vaatweefsel in 'n aantal bondels wat in die lamina die hoofare vorm.

ABSTRACT

THE NODE AND PETIOLE MORPHOLOGY OF THE SOUTH AFRICAN REPRESENTATIVES OF THE GENERA ADENOLOBUS (HARV.) TORRE & HILLC., BAUHINIA L., PILIOSTIGMA HOCHST. AND TYLOSEMA (SCHWEINF.) TORRE & HILLC.*

The stems of the genera *Adenolobus, Bauhinia, Piliostigma* and *Tylosema* have typically trilacunar nodes and the leaves are borne alternately on the stem. The lateral leaf traces branch and supply the stipules with vascular tissue before they unite with the median leaf trace.

The vascular tissue of the petiole is discussed under the following zones: first transition zone, pulvinary zone, second transition zone, median zone, third transition zone and distally

thickened zone.

The arrangement of vascular tissue in the petiole is characteristic for each species. This vascular tissue undergoes considerable anastomosing and branching from the pulvinus to the distally thickened end where the vascular tissue divides into a number of bundles which give rise to the main veins of the palmately veined lamina.

1 INLEIDING

Die algemene opvatting van die begrip knoop is dat dit daardie gedeelte van 'n stingel verteenwoordig wat die grens tussen twee opeenvolgende litte vorm. Verder is dit die posisie op die stingel waar blare gedra word en wat in sommige

^{*} Gedeelte van 'n verhandeling vir die M.Sc-graad in Algemene Plantkunde aan die Universiteit van Pretoria, deur eersgenoemde outeur.

Vir publikasie aanvaar 11 September 1975.

gevalle herkenbaar is vanweë ringvormige verdikkings of littekens waar blare voorheen gedra is. By die toepassing van die begrip knoop lê die probleem by die presiese afbakening van die gebied. Daar kan tereg met Howard (1970) saamgestem word dat hierdie afbakening moeilik is want ringvormige verdikkings is by die meeste stingels afwesig en blaarlittekens mag groter word met die plant se toename in ouderdom en dan 'n breë strook op die stingel verteenwoordig.

Alhoewel dit relatief maklik is om by 'n beblaarde takke uitwendig die posisies van die knope vas te stel, word dit moeiliker om die grense daarvan op grond van die anatomie van die stingel af te baken en veral op grond van die anatomie, tussen knope en litte te onderskei. Daarom is daar met hierdie studie gepoog om by 'n paar verteenwoordigers van die Caesalpiniaceae die anatomiese knope en litte vas te stel en 'n verband te vind tussen die aftakposisies van die blaarspore en die posisies van die blare op die stingel. Met hierdie doel voor oë is die anatomie van die stingels en blaarstele van die Suid-Afrikaanse verteenwoordigers van die genera Adenolobus, Bauhinia, Piliostigma en Tylosema ondersoek. Aandag is veral aan die knope en die verdere verloop van die vaatweefsel vanaf die knoop tot in die lamina van die blaar gegee.

2 MATERIAAL EN METODE VAN ONDERSOEK

Volwasse, vars materiaal van al die betrokke plantsoorte is in die veld versamel en in form-aseet-alkohol (FAA) vir minstens 48 uur gefikseer (Johansen, 1940). Die gefikseerde materiaal is volgens die T B A-metode van Sass (1966) gedehidreer en met Paraplastwas geïmpregneer. Draaimikrotoomsneë, met 'n dikte van tussen 6 μm en 10 μm , is van knope, litte en blaarstele gemaak en met safranien en kleurvaste groen, of safranien en hematoksilien, of toluïdienblou gekleur. In al die gevalle is seriesneë van die litte, knope en blaarstele gemaak sodat die verloop van die vaatweefsel gevolg kon word.

Die volgende soorte is ondersoek:-

Adenolobus garipensis (E. Mey.) Torre & Hillc.;

Adenolobus pechuelii (Kuntze) Torre & Hillc.;

Bauhinia bowkeri Harv.;

Bauhinia galpinii N.E. Br.;

Bauhinia macrantha Oliv.;

Bauhinia natalensis Oliv.;

Bauhinia petersiana Bolle;

Bauhinia tomentosa L.:

Bauhinia urbaniana Schinz;

Piliostigma thonningii (Schumach.) Milne-Redhead;

Tylosema esculentum (Burch.) Schreiber; en Tylosema fassoglensis (Schweinf.) Torre & Hillc.

3 Morfologie van die Knoop

By al die ondersoekte soorte word die blare afwisselend op die stingels gedra en verloop die vaatweefsel aan elke blaar vanuit 'n trilakunêre knoop. Voordat die laterale blaarspore egter by die mediane blaarspoor aansluit, vorm elk 'n sytak wat na die steunblare verloop. Steunblare word meesal met 'n trilakunêre knoop geassosieer. Waar die blaarspore die stelé verlaat, bult die stingel uit (Fig. 1) en kan die blaarspore in die meeste gevalle uitwendig as riwwe op die stingels waargeneem word. Nader na die blaarbasis word die riwwe duideliker.

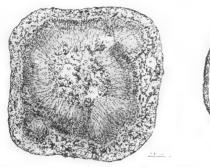




Fig. 1.

Die stingel van *Piliostigma thonningii* soos in dwarsdeursnee gesien, om die bou van 'n trilakunêre knoop te toon K—korteks; Lb—laterale blaarspoor; M—murg; Mb—mediane blaarspoor,

Fig. 2.

Die stingel van *Tylosema esculentum* soos in dwarsdeursnee gesien om die bou van 'n trila-kunêre knoop te toon Lb—laterale blaarspoor; M—murg; Mb—mediane blaarspoor.

Die volgende gemeenskaplike kenmerke is by die trilakunêre knope van die verskillende soorte gevind:

- (i) die mediane blaarspore is in al die gevalle groter as die laterale blaarspore;
 en
- (ii) die mediane blaarspore ontstaan in al die gevalle meer proksimaal in die lit as die laterale blaarspore.

Uit die ondersoek blyk dit dat die mediane blaarspore alleen by soorte van die genus *Tylosema* die stelé voor die laterale blaarspore verlaat (Fig. 2). Met die uitsondering by *Bauhinia tomentosa* waar al drie die blaarspore in sommige gevalle die stelé gelyktydig verlaat, is dit die reël by die ondersoekte soorte dat die laterale blaarspore voor die mediane blaarspore die stelé verlaat.

Sodra die laterale blaarspore, wat deurgaans kollateraal bly, die stelé verlaat, verloop hulle in die korteks van die stingel in die rigting van die mediane blaarspoor om daarby aan te sluit. Alleen laterale blaarspore van die *Tylosema*soorte verloop feitlik horisontaal om die stelé na die mediane blaarspoor (Fig. 3), terwyl die laterale blaarspore by die oorblywende soorte skuins na bo rondom die stelé verloop (Fig. 1).

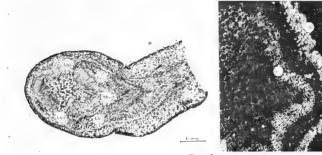


FIG. 3.

Die stingel van *Tylosema esculentum* soos in dwarsdeursnee gesien om die horisontaalverlopende laterale blaarspore (Lb) te toon Lbo—laterale blaaropening; Mbo—mediane blaaropening; P—pulvinus (tussen pyltjies)

Fig. 4.

'n Gedeelte van 'n dwarsdeursnee van die stingel van *Bauhinia macrantha* soos onder gepolariseerde lig gesien om 'n laterale blaarspoor (Lb) te toon wat volledig deur sklerenchiemweefsel (S) omgewe is X—xileem.

Baie min versterkingsweefsel kom by die blaarspore voor. In die geval van Bauhinia petersiana, B. urbaniana en B. macrantha is veral die laterale blaarspore volledig deur 'n laag sklerenchiemweefsel omgewe (Fig. 4) terwyl hierdie meganiese skede by die blaarspore van die oorblywende soorte slegs gedeeltelik sklerenchimaties is (Fig. 5). Die sklerenchiemweefsel is nie aaneenlopend vanaf die aftakking van die blaarspore tot in die blaarlamina nie, want in geen geval kom sklerenchiemweefsel in die pulvinus rondom die vaatweefsel voor nie.

Dit is opvallend dat die deursnee van die blaarspore by Adenolobus garipensis en A. pechuelii min of meer onveranderd bly nadat hulle die stelé verlaat het, terwyl al drie blaarspore by Piliostigma thomingii na aftakking uit die stelé

vergroot. By soorte van die genera *Bauhinia* en *Tylosema* vergroot slegs die mediane blaarspore. Hierdie vergroting impliseer die vermeerdering in hoeveelheid vaatweefselmateriaal van die betrokke blaarspore.



Fig. 5.
'n Gedeelte van 'n dwarsdeursnee van de stingel van Piliostigma thonningii om 'n laterale blaarspoor (Lb) te toon wat gedeeltelik deur sklerenchiemweefsel (S) omgewe is E—epidermis; K—korteks; Lbo—laterale blaaropening.

Fig. 6.
Distale verdikking van 'n blaarsteel van Bauhinia galpinii.

Volgens Esau (1965), is die inwendige "knoop" by 'n stingel daardie deel van die stelé wat met die vereniging van die vaatweefsel van een of meer blare geassosieer word. Dit kan dus geïnterpreteer word as dié deel van die stingel vanwaar die blaarspoor begin aftak tot waar dit die stelé verlaat. Hoe verder proksimaal van die organografiese knoop 'n blaarspoor dus in die stelé begin aftak, hoe langer is die anatomiese knoop. By die ondersoekte soorte is gevind dat die mediane blaarspoor van 'n bepaalde knoop al by die voorafgaande knoop sigbaar is (Fig. 2). Elke mediane blaarspoor ontstaan dus verder proksimaal in die stingel as die posisie waar die blaarspore by die voorafgaande knoop die stelé verlaat en verloop dan vir meer as een organografiese lit in die stelé langs. Hiervolgens is daar dan 'n oorvleueling van die knoopgrense en stem die anatomiese knope nie met die organografiese knope ooreen nie. Daarom meen sommige outeurs soos Howard (1970), dat die grootste deel van 'n stingel uit vaatbondels bestaan wat van die blare afkomstig is, omdat die vaatsisteem in blaarbasisse hoofsaaklik basipetaal differensieer, afwaarts in die stingel verloop en by ander blare se spore aansluit om 'n eenheid naamlik die stelé te vorm.

Indien egter gelet word op 'n knoop in die klassieke anatomiese sin naamlik slegs as die gebied van blaaropeninge (Howard, 1974), dan beslaan die knoop

'n kleiner gebied as volgens Esau (1965) se beskouing en kom die anatomiese knoop by die ondersoekte soorte na aan die organografiese knoop voor. Dit het tot gevolg dat daar dan wat die ondersoekte soorte betref, 'n logiese verband is tussen die aftakposisie van 'n blaar se blaarspore en die plek waar hulle die stingel verlaat.

4 MORFOLOGIE VAN DIE BLAARSTEEL

4.1 Uitwendig

Die blaarsteel by die ondersoekte soorte is lynvormig maar die lengte daarvan varieer inter- sowel as intraspesifiek. Met die uitsondering van Adenolobus garipensis en A. pechuelii het die proksimale deel van die blaarsteel 'n pulvinus.

Distaal waar die blaarsteel in die lamina oorgaan, kom daar 'n soortgelyke maar breër verdikking voor waaruit die hoofare van die lamina ontspring (Fig. 6—tussen pyltjies). Volgens Eames (1961) is hierdie verdikking tussen die blaarsteel en lamina die gevolg van 'n versmelting van pinnas om 'n enkelvoudige blaar te vorm wat as gemodifieerde saamgestelde blaar beskou kan word. Hierdie beskouing word ook deur Croizat (1973) gehuldig.

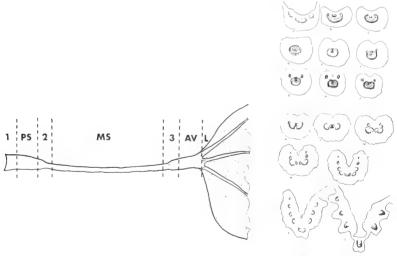


Fig. 7.

'n Skematiese voorstelling van die onderverdeling van 'n blaarsteel in die verskillende sones 1—eerste oorgangsone; 2—tweede oorgangsone; 3—derde oorgangsone; L—lamina. PS—pulvinêre sone; MS—mediane sone; AV—distale verdikking.

Fig. 8

Lyndiagramme van opeenvolgende akropetale dwarsdeursneë van 'n blaarsteel van *Bauhinia bowkeri* om die verloop, anastomosering en vertakking van die vaatbondels te toon.

4.2 Inwendig

Met die verloop van die vaatweefsel in die blaarsteel, vind daar gedurig vertakking en versmelting van vaatweefsel plaas met die gevolg dat verskillende rangskikkingspatrone in 'n dwarsdeursnee van 'n blaarsteel gesien word. In twee gedeeltes nl. die middelste gedeelte van die pulvinus en die middelste gedeelte van die blaarsteel as geheel, bly die vaatweefsel egter vir 'n kort afstand onveranderd en ondergaan geen anastomosering of vertakking nie. Hierdie twee dele word vir die doel van hierdie studie onderskeidelik die pulvinêre en mediane sones genoem en verteenwoordig die dikste en dunste dele van die blaarsteel, terwyl die mediane sone ook die langste deel van die blaarsteel uitmaak (Fig. 7). Die drie oorblywende dele van die blaarsteel word as oorgangstreke beskou waar daar 'n herrangskikking van vaatweefsel plaasvind en word vir hierdie doel oorgangsones genoem (Fig. 7).

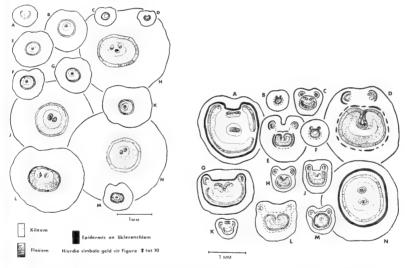


Fig. 9.

Lyndiagramme van dwarsdeursneë van pulvinêre sones van blaarstele van al die ondersoekte soorte

A—A. pechuelii; B—B. galpinii; C—B. natalensis; D—A. garipensis; E—B. tomentosa var. tomentosa; F—B. urbaniana; G—B. macrantha; H—P. thonningii; J—T. esculentum; K—B. bowkeri; L—B. petersiana; M—B. tomentosa var. glabrata; N—T. fassoglensis.

Fig. 10.

Lyndiagramme van dwarsdeursneë van die mediane gedeelte van blaarstele van al die ondersoekte soorte

A—T. esculentum; B—A. garipensis; C—B. tomentosa var. tomentosa; D—P. thonningu; E—B. bowkeri; F—A. pechuelii; G—B. petersiana; H—B. tomentosa var. glabrata; J—B. urbaniana; K—B. natalensis; L—B. galpinii; M—B. macrantha; N—T. fassoglensis.

Alhoewel die aaneenskakeling en vertakking van die vaatweefsel in die blaarstele van al die soorte grootliks ooreenstem, kan daar tog basiese verskille by die vier ondersoekte genera aangedui word.

4.2.1 Eerste Oorgangsone (Fig. 7 sone 1 en Fig. 8A, B & C)

Hierdie sone strek vanaf die blaaropeninge in die stelé tot by die pulvinêre sone en word gekenmerk deur die aansluiting van die laterale blaarspore by die mediane blaarspoor. Dit geskied in die blaarbasis nadat vaatweefsel vanaf die laterale blaarspore na die steunblare afgetak het. Die aansluiting vind aan weerskante maar effens adaksiaal by die mediane blaarspoor plaas, sodat 'n halfmaanvormige vaatbondel ontstaan met die konkawe kant adaksiaal (Fig. 8A, B & C). Met die uitsondering van soorte van die genus *Adenolobus*, gaan hierdie aansluiting gepaard met die aftakking van adaksiale vaatweefsel in die blaarvoet (Fig. 8B).

4.2.2 Pulvinêre Sone (Fig. 7 sone PS en Fig. 8D)

Nadat die laterale en mediane blaarspore by mekaar aangesluit het, verloop dit in die pulvinêre sone wat kenmerkend vir elke genus is (Fig. 9). By die genus *Adenolobus* is die enigste heroriëntasie van die vaatweefsel ná aansluiting van die blaarspore by mekaar dat die halfmaanvormige struktuur meer silindries en smaller word (Fig. 9A & D). By soorte van die genera *Bauhinia* (Fig. 8D & Fig. 9B, C, E, F, G, K, L & M), *Piliostigma* (Fig. 9H) en *Tylosema* (Fig. 9J & N) sluit die halfmaanvormige vaatbondel adaksiaal, waartydens een tot drie kleiner vaatbondels na 'n sentrale posisie aftak en ingesluit word deur die vaatsilinder wat hier ontstaan.

By Bauhinia petersiana (Fig. 9L), Tylosema esculentum (Fig. 9J) en T. fassoglensis (Fig. 9N) ontstaan twee sentrale vaatbondels in teenstelling met drie by Piliostigma thonningii (Fig. 9H) en net een elk by sommige van die oorblywende soorte. Slegs by Bauhinia natalensis (Fig. 9C) kom geen sentrale vaatbondel binne die vaatsilinder voor nie.

Hierdie sentraalgeleë kollaterale vaatbondels ontstaan as sytakke van die oorspronklike laterale blaarspore. Hulle kan afsonderlik van mekaar deur die blaarsteel verloop of versmelt om 'n enkele en groter sentrale vaatbondel te vorm. By soorte van die genus *Tylosema* verander hierdie sentraalgeleë kollaterale vaatbondels in die mediane sone na amfivasale vaatbondels (Fig. 10A & N).

4.2.3 Tweede Oorgangsone (Fig. 7 sone 2 en Fig. 8E, F & G)

Kenmerkend vir die tweede oorgangsone is dat die vaatsilinder van die pulvinêre sone, in bykans al die gevalle adaksiaal open (Fig. 8E, F & G), waartydens een of meer addisionele kollaterale vaatbondels aftak. Sommige van hierdie bondels swaai weg van die hoofvaatbondel en neem 'n adaksiale

of laterale posisie in (Fig. 8G). By die meeste van die soorte ontstaan daar tydens die oopgaan van die vaatsilinder een kollaterale vaatbondel wat in 'n adaksiale posisie bokant die sentrale vaatbondel bly (Fig. 8E & F), terwyl twee verdere adaksiale vaatbondels van die hoofvaatbondel aftak en na 'n laterale posisie verskuif (Fig. 8F, G & H). Hierdie laterale vaatbondels bied addisionele strukturele versterking aan die blaarsteel en verenig eers weer in die derde oorgangsone met die hoofvaatbondel. Geen laterale vaatbondels kom by soorte van die genus *Tylosema* voor nie.

4.2.4 Mediane Sone (MS) (Fig. 7 sone MS en Fig. 8H)

Die uitbeelding van die vaatweefsel in die mediane sone van die blaarsteel van al die ondersoekte soorte is diagnosties van aard sodat die soorte op grond hiervan van mekaar onderskei kan word (Fig. 10). Alhoewel die vaatweefselrangskikking in die blaarsteel van die *Tylosema*-soorte opvallend van mekaar verskil, stem dit tog in 'n groot mate met die algemene patroon van die ondersoekte soorte ooreen.

Die uitbeelding van die vaatweefsel in hierdie sone is U-balkvormig (Fig. 10) wat voldoende meganiese versterking aan die blaarsteel bied vir die dra van die lamina, maar nogtans elasties genoeg is om te kan buig of wring.

Die laterale vaatbondels is nie kenmerkend vir 'n adaksiale groef in die mediane sone van die blaarsteel nie. So byvoorbeeld is die mediane sone by *Bauhinia bowkeri* (Fig. 10E) uitwendig duidelik gegroef, by *B. natalensis* en *B. tomentosa* (Fig. 10C & K) minder opvallend gegroef en ontbreek 'n adaksiale groef by *Adenolobus pechuelii* (Fig. 10F), terwyl by al hierdie soorte laterale vaatbondels voorkom

In teenstelling met die laterale vaatbondels wat feitlik oor die hele lengte van die mediane sone onveranderd bly, ondergaan die adaksiale en sentrale vaatbondels van sekere soorte anastomosering wat dan tipies vir daardie soorte is. Die verskillende posisionele veranderings van die adaksiale en sentrale vaatbondels is soos volg:-

- (i) die vaatbondels sluit weer by die hoofvaatbondel aan om 'n enkele Uvormige vaatbondel te vorm (Fig. 10E & L); of
- (ii) die vaatbondels sluit weer by die hoofvaatbondel aan om 'n vaatsilinder te vorm (Fig. 10B, D, F & M); of
- (iii) die vaatbondels verloop, soos die laterale vaatbondels, afsonderlik deur die hele mediane sone (Fig. 10C, G, H, J & K).

Vir *Tylosema esculentum* en *T. fassoglensis* is een of twee sentraal-geleë amfivasale vaatbondels wat deur die vaatsilinder van die mediane sone ingesluit word (Fig. 10A & N), kenmerkend.

Die vaatbondelskede in die mediane sone is geheel of gedeeltelik sklerenchimaties (Fig. 10) en dit is opvallend dat sklerenchiemweefsel in die blaarsteel slegs in die mediane sone rondom die vaatbondel voorkom. Verder is die vaatbondelskede eers weer aan die einde van die distale verdikking, waar die hoofare aftak, gedeeltelik sklerenchimaties (Fig. 8Q).

4.2.5 Derde Oorgangsone (Fig. 7 sone 3) en Distale Verdikking (Fig. 7 sone AV)

Die heroriëntering van vaatweefsel in die blaarsteel vanaf die mediane sone tot in die distale verdikking, word gekenmerk deur relatief baie anastomoses en vertakkings. In al die gevalle word die vaatbondels breër en platter en verdeel later in 'n aantal kleiner vaatbondels wat elk deel van 'n hoofaar uitmaak.

Waar daar laterale vaatbondels in die blaarsteel voorkom, sluit hulle lateraal by die U-vormige hoofvaatbondel aan en hierdie aansluiting gaan gepaard met die aftak van sentrale vaatbondels, of indien daar reeds is, addisionele sentrale vaatbondels (Fig. 8J & K). By al die soorte kom dus sentrale vaatbondels gedurende die derde oorgangsone, adaksiaal van die hoofvaatbondel, in die blaarsteel voor. Hierdie vaatbondels verdeel in die distale verdikking en dra saam met die verdelende hoofvaatbondel by om die vaatbondels van die hoofare in die lamina te vorm (Fig. 8M, N & O).

Dit blyk egter dat die sentrale vaatbondels by die genus *Bauhinia* na 'n adaksiale posisie skuif en versmelt om in die meeste gevalle slegs aan die mediane hoofaar in die lamina oorsprong te gee (Fig. 8N, O & P). Daar is ook gevalle bekend waar die sentrale vaatbondels nie net aan die mediane hoofaar oorsprong gee nie, maar ook bydra tot die vaatweefsel van die hoofare direk weerskante van die mediane hoofaar, soos by *Adenolobus pechuelii* en *Piliostigma thonningii*.

Waar 'n mukro by die blare voorkom, is gevind dat die mukro ook van vaatweefsel voorsien word en wel deur die mediane hoofaar wat daarin eindig.

5 BESPREKING

Alhoewel daar 'n noue assosiasie tussen die knope van 'n stingel en die blare wat daarop voorkom bestaan, kan die term "knoop" nie ewe maklik op beide die uitwendige en inwendige morfologie toegepas word nie. Die terme knoop en lit het hul beslag in die organografie gevind en die huidige toepassing daarvan is duidelik. Wat die anatomie egter betref, openbaar die vaatweefsel meesal 'n patroon wat nie direk met dié van die organografie ooreenstem nie. In hierdie verband word verwys na plante waar die blaarspore, na verlating van die stelé, vir een of meer litte in die korteks langs verloop voordat dit na buite in 'n blaar in strek.

Indien slegs dié gedeelte van die stingel waar blaarspore die stelé verlaat, as die anatomiese knoop beskou word, lê die anatomiese en organografiese knope en litte van die ondersoekte soorte, na aan mekaar. Die kort blaarspore, wat veral in die geval van die genus *Tylosema* horisontaal om die stelé verloop,

bring die anatomiese en organografiese knope feitlik regoor mekaar. In hierdie geval is die anatomiese en organografiese knope vir 'n bepaalde blaar dan baie nou met mekaar geassosieer omdat hulle so na aan mekaar geleë is. Ongelukkig kan die term "knoop" nie deurgaans in die morfologie só op alle plante toegepas word nie.

Wat die vaatweefsel in die blaarsteel betref, is dit interessant om daarop te let dat die vaatbondels in die pulvinêre sone van al die ondersoekte soorte, grootliks met die bou en vorm van die vaatbondels in die distale verdikking ooreenstem (vergelyk Fig. 8C & Q). Daarom wil dit voorkom of die distale verdikking van 'n blaarsteel uit versmelte pulvinusse van pinnas bestaan en kan dan beweer word dat die ragis van die saamgestelde blaar nie ontwikkel het nie en al die pulvinusse so bymekaar gehou het. Hierdie postulering onderskryf die bewering dat die blare van die genus *Bauhinia* en verwante genera 'n oorgangstadium tussen saamgestelde en enkelvoudige blare verteenwoordig (Eames, 1961).

Alhoewel die stingels en blare van die ondersoekte soorte baie oorspronklike kenmerke toon, is dit 'n ope vraag of hulle wel oorspronklik is. Nogtans is dit interessant om te vind dat daar 'n noue assosiasie tussen die organografiese en anatomiese knope en litte en die posisie, bearing en vaatweefsel van die blare is.

Die meeste resente opvatting van 'n knoop (Howard, 1974) is dat dit 'n meristematiese streek op die stingel verteenwoordig, die sogenaamde "nodal locus", wat by primitiewe plante 'n breë strook, selfs rondom die stingel, en by meer gevorderde plante 'n smal en kort strook, vergelykbaar met die blaarmerk, verteenwoordig. In hoeverre bied ons huidige morfologiese begrippe egter voldoende oplossings en verklarings vir probleme? Howard (1974) stel die saak soos volg:

"Attempts to place in a single phylogenetic sequence the nodal gaptrace area; alternate, opposite or whorled leaves; simple or compound leaves; sessile or petiolate leaves; stipulate or exstipulate leaves, etc., are fundamentally useless. Such characteristics of modern plants must be recognised as mid points in the evolution of the modern leaf. The chances are that such morphological expressions are not sequential, but parallel development from a very simple ancestral type."

6 DANKBETUIGING

Die hoof en personeel van die Navorsingsinstituut vir Plantkunde asook van die Departement Plantkunde aan die Universiteit van Pretoria word bedank vir hulp en alle middele wat ter beskikking gestel is om hierdie studie suksesvol te voltooi.

Die navorsing is finansieel deur die Navorsings- en Publikasiekomitee van die Universiteit van Pretoria en die WNNR ondersteun.

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NOTE ON CYTOKININS IN THE XYLEM SAP OF PROTEA COMPACTA

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ABSTRACT

Partition chromatography on Sephadex LH-20 indicated that zeatin is probably the major cytokinin present in the transpiration stream of *Protea compacta* seedlings.

UITTREKSEL

NOTA AANGAANDE SITOKINIENE IN DIE XILEEMSAP VAN *PROTEA COMPACTA* Met behulp van partisie-chromatografie op Sephadex LH-20 is gevind dat zeatien waarskynlik die belangrikste sitokinien in die transpirasiestroom van *Protea compacta* saailinge is.

A number of reports have indicated that endogenous cytokinins are involved in the growth and development of proteaceous species (Brown and Van Staden, 1973; Van Staden and Brown, 1973). As very little information is available as to the nature of the cytokinins involved an attempt was made to learn more about the cytokinin complement of *Protea compacta* R.Br.

To simplify investigation the xylem sap from six month old seedlings was analyzed. Xylem sap was assayed as it is well known that the roots of plants act as a site of cytokinin synthesis and that these substances are translocated in the transpiration stream (Kende and Sitton, 1967; Yoshida *et al.*, 1971). In addition xylem sap does not contain many impurities which necessitate complicated purification techniques.

Plants growing in pots were decapitated 2 cm above soil level. Root exudate was collected for 24 hours by means of a rubber tube attached to the stem. The sap was collected, filtered and taken to dryness under vacuum at 35°C. The residue was washed with 10 ml 80% ethanol, filtered, concentrated to 2 ml and separated on a Sephadex LH-20 column (2.5 x 90 cm). The column was eluted with 35% ethanol at a flow rate of 15 ml/hour. This technique of fractionation has been shown to be a reliable and reproducible method of cytokinin separation (Armstrong et al., 1969). It is also most useful for the identification of cytokinins in plant material (Van Staden and Drewes, 1975). Forty ml fractions were collected from the column. These were dried in air and assayed for cytokinin activity with the soybean bioassay (Miller, 1965).

^{*} The authors wish to acknowledge the financial assistance of the C.S.I.R. Pretoria. Accepted for publication 5th August, 1975.

Three peaks of activity, that co-eluted with authentic cytokinins, were recorded in the root exudate (Fig. 1). The results indicate that zeatin appears to be the major translocation form of cytokinin in the xylem sap of P. compacta seedlings. However, small amounts of zeatin riboside and $6-(\triangle^2$ -isopentenylumino) purine (2iP) were also apparently present. The finding that zeatin is probably the major cytokinin in the xylem sap of P. compacta is contrary to Letham's (1974) suggestion that zeatin riboside is the major form in which cytokinin is translocated from the roots of plants. It is however noticeable that in all experiments, where zeatin riboside predominated, the root exudate was partitioned against butanol prior to fractionation. Although it does not form part of the present investigation, evidence is available which indicates that zeatin is not totally recovered when plant extracts are partitioned against butanol.

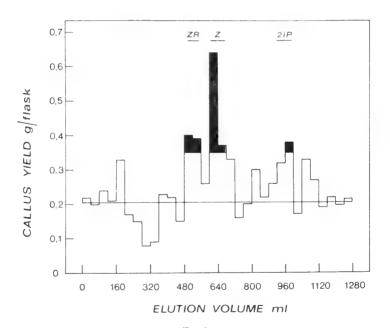


Fig. 1. Soybean bioassay of 50 ml of root exudate of *Protea compacta* fractionated on Sephadex LH-20. Z = zeatin, ZR = zeatin riboside, $2iP = 6 - (^2 - isopentenylamino)$ purine.

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INITIATION AND GROWTH OF LEUCOSPERMUM CORDIFOLIUM CALLUS

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ABSTRACT

Callus was initiated from the cotyledons and hypocotyls of *Leucospermum cordifolium* seedlings. A comparative study of four media with respect to their ability to support the growth of this callus revealed that Miller's (1965) medium was best suited for this purpose.

UITTREKSEL

INISIASIE EN GROEI VAN LEUCOSPERMUM CORDIFOLIUM KALLUS

Kallus is van die saadlobbe en hipokotiele van Leucospermum cordifolium saailinge geïnisieer. 'n Vergelykende studie van vier media ten opsigte van hulle vermoë om die groei van dié kallus te onderhou het getoon dat die medium van Miller (1965) die beste hiertoe instaat is.

INTRODUCTION

Propagation by tissue culture is an ideal and widely used method for the vegetative multiplication of particular clones of plants which are difficult to propagate by standard horticultural techniques. Very small pieces of plant tissue e.g. seeds, embryos, stems, midribs or inflorescences have been cultured to establish callus which can subsequently be used for micro-propagation of the plant concerned (Hartmann and Kester, 1975).

A number of species of the South African Proteaceae, in particular *Oro-thamnus zeyheri*, are extremely rare. On two occasions it has been thought to be extinct. At present, very few plants of this monotypic genus are found in the wild. Attempts to obtain seed by hand pollination of flowers proved successful. However, germination of this seed has been poor and sporadic (Van der Merwe, 1974). Because of the success of tissue culture techniques in propagation of other horticulturally desirable plants (Morel, 1964; Romberger *et al.*, 1970; Ziv *et al.*, 1970; Ben-Jaacov and Langhans, 1970; Pierik *et al.*, 1974) these techniques appear to be ideally suited to overcome the propagation difficulties of this rare plant. In view of the limited material available initial experiments were conducted on a closely related plant, *Leucospermum cordifolium*. This was done with the object of establishing means of initiating callus and the selection of a nutrient medium best suited to support its continuous growth.

EXPERIMENTS AND DISCUSSION

Leucospermum cordifolium (Salisb. ex Knight) Fourcade seed, obtained from the Forestry Department, Pretoria, was used as experimental material. After scraping off the thin, brittle, outer pericarp seeds were surface sterilized for 30 minutes in a saturated calcium hypochlorite solution. Following this they were immersed in 95% ethanol for 10 minutes and then thoroughly rinsed with sterile distilled water. Previous experiments have shown that germination of this species is retarded by the presence of the hard, woody, inner pericarp as it restricts oxygen uptake by the embryo (Van Staden and Brown, 1973). As a result the woody pericarp was removed from all surface sterilized seed under aseptic conditions. The excised embryos were transferred to 100 ml flasks containing 50 ml of Hoagland's solution solidified with 1% agar. The flasks were kept in a germinator and maintained at a daily temperature regime of 10°C for 16 hours followed by 20°C for 8 hours. Sterilization of the embryos was 64% effective. Sterile embryos started germinating after 15 days. After 30 days 69% of these embryos had germinated and developed into seedlings. When six weeks old the cotyledons and hypocotyls were excised from the seedlings and the explants cultured on Miller's (1965) soybean medium. In addition to the basic salts and vitamins sucrose (3%), NAA (2 mg/1), coconut milk (10%) and Difco Bacto-agar (1%) were incorporated into the medium. The pH of the medium was adjusted to 5,8 and 40 ml dispensed into 100 ml flasks which were then autoclaved. Cultures containing explants were maintained under continuous light from white fluorescent tubes at 26 + 1°C. Both cotyledonary and hypocotyl explants showed signs of callus initiation after eight weeks of culturing. This callus grew slowly and required sub-culturing approximately every six weeks.

Callus of cotyledonary and hypocotyl origin was very different in appearance: that from the cotyledons was hard and green, while in contrast callus from hypocotyls was white, soft and friable in appearance (Fig. 1A).

Although the original choice of medium proved most fortunate in that it was capable of initiating and supporting the growth of *Leucospermum* callus, it was nevertheless essential to establish whether other media could not accelerate the rate of callus growth. As insufficient hypocotyl callus was available, subsequent experiments were carried out with cotyledonary callus only. All experiments were repeated twice and treatments replicated ten times. The constituents of the media tested for their ability to support the growth of *Leucospermum* callus are given in Table 1. Sucrose (3%), Difco Bacto-agar (1%) and NAA (2 mg/1) were incorporated into all media. The efficacy of coconut milk (10%) was compared with the naturally-occurring cytokinin zeatin (10 μ g/1) as preliminary experiments indicated that kinetin was less effective in maintaining callus growth. In addition it is now known that coconut milk contains zeatin

(Van Staden and Drewes, 1975) and that this cytokinin is present in proteaceous species (Brown and Van Staden, 1973; Van Staden and Davey, 1976). Before autoclaving, the pH of each medium was adjusted to 5,8 and 40 ml dispensed

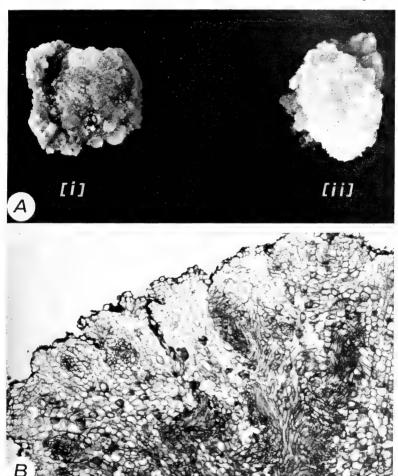


Fig. 1A.

Appearance of *Leucospermum* callus of (i) cotyledonary and (ii) hypocotyledonary origin.

Fig. 1B.

Islets of meristematic cells in callus grown on Miller's (1965) medium in the presence of zeatin.

into 100 ml flasks. One piece of callus (+ 30 mg) was transferred to each flask and allowed to grow for 60 days under the conditions described earlier. At the end of this period the callus was weighed. From the data presented in Fig. 2 it is obvious that Miller's medium was most beneficial for the growth of Leucospermum callus. No simple explanation can be given for these results. A comparison of the composition of the media investigated (Tables 1 and 2) indicates that the vitamin concentration, especially thiamine, nicotinic acid and pyridoxine of Miller's medium was much lower than that used by Murashige and Tucker (1969) and Schenk and Hildebrandt (1972). The micro-nutrient composition of most media showed only slight variation. In the case of Heller's medium however, the trace element molybdenum was omitted. This together with the fact that nitrogen was supplied as nitrate only may account for the poor growth of the callus on this medium, especially as this essential element is required for nitrate reduction (Steward and Durzan, 1965). A further contributing factor may be the fact that except for potassium the concentrations of essential macronutrient elements supplied are extremely low (Table 2). The major differences recorded (Fig. 2) between the media of Murashige and Tucker (1969), Schenk and

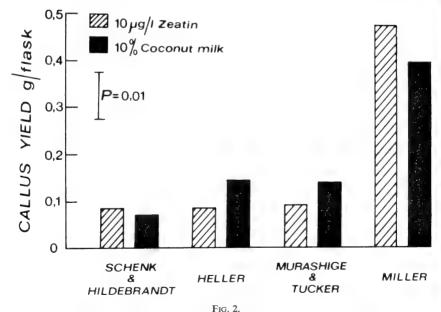


Fig. 2.

The effect of different nutrient media on the growth of *Leucospermum* callus.

TABLE 1. Constituents of media tested for their ability to maintain the growth of *Leucospermum* callus.

	Weight of constituents in final medium (mg/liter)			
Constituent	Heller (1953)	Murashige and Tucker (1969)	Miller (1965)	Schenk and Hildebrandt (1972)
Macro-nutrients NH ₃ NO ₃	750 600 125 75 —	1 650 1 900 170 — — 440 — 370	1 000 1 000 65 300 - 500 71,5	300 2 500 ———————————————————————————————————
Micro-nutrients FeC1 ₃ ·6H ₂ O	1,0 1,0 1,0 0,01 0,03 0,01 0,03 0,03	40,0 6,2 8,6 22,3 0,025 — 0,25 0,83 0,025 —	13,2 1,6 3,8 14,0 0,35 0,1 	40,0 5,0 1,0 10,0 0,2 — 0,1 1,0 0,1 —
Vitamins Myo-inositol	Vitamins of Miller (1965) added	100 10 5 10 2	100 0,1 0,5 0,1	1 000 5 5 5

Hildebrandt (1972) and Miller (1965) can probably be attributed to differences in macro-nutrient composition and/or the ratio of ammonia nitrogen: nitrate nitrogen incorporated into them. It has previously been shown that a balanced supply of nitrate and ammonia salts is beneficial to the growth of certain types of callus (Shantz and Steward, 1959). In Table 2 it can be seen that the media of Murashige and Tucker (1969) and Miller (1965) have roughly similar ratios of ammonia: nitrate. In contrast that of Schenk and Hildebrandt (1972) contains

a very low concentration of ammonia nitrogen. This low concentration may possibly explain its detrimental effect on the callus growth. The major difference, apart from their vitamin complement, between Murashige and Tucker's and Miller's media is that the latter contained substantially lower levels of macronutrient elements (Table 2), the exception being phosphorus which was present in a higher concentration.

The callus pieces grown on Miller's medium in the presence of zeatin not only grew well, but on their lower surface contained small dome-shaped outgrowths. This material was fixed in formalin-acetic acid-alcohol, dehydrated and embedded in the usual manner for histological investigation.

The callus proved to be composed of parenchymatous cells. In places islets of meristematic tissue were observed in which the cells contained a dense cytoplasm. Within these islets vascular tissue, mainly phloem, had differentiated (Fig. 1B). In view of the fact that in other plants these islets develop into adventitious buds or "embryoids" (Bajaj and Mäder, 1974), it seems reasonable to assume that *Leucospermum* callus may have the same ability. Whether this will happen depends on the balance of hormones supplied to this tissue. This problem is currently under investigation.

ACKNOWLEDGEMENTS

The financial support of the C.S.I.R., Pretoria, is gratefully acknowledged.

Table 2. Macro-nutrient element composition of media compared for their ability to support the growth of Leucospermum callus. (Concentration of elements in final medium. mg/l)

Element	Heller (1953)	Murashige and Tucker (1969)	Miller (1965)	Schenk and Hildebrandt (1972)
N P K Ca Mg S	98,8 24,8 392,3 27,0 24,8 32,4	840,0 39,0 782,0 121,0 36,8 52,3	547,8 68,3 120,0 84,7 7,0 9,3	382,5 80,8 964,3 54,4 38,9 51,9
Ratio of NH ⁺ :NO ₋	Nitrogen as NO—3 only	1:1,9	1:2,1	1:9,5

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MICROSPOROGENESIS AND -GAMETOGENESIS IN STRELITZIA REGINAE AIT.

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ABSTRACT

The anther of *Strelitzia reginae* is tetrasporangiate with a persistent epidermis. The endothecium develops fibrous thickenings, the middle layers are ephemeral and the cells of the glandular tapetum are frequently binucleate.

Divisions of the microspore mother cells are of the successive type and the microspore

tetrads are isobilateral, T-shaped and linear.

The spherical, smooth-walled pollen grains are uninucleate at dehiscence.

UITTREKSEL

MIKROSPOROGENESE EN -GAMETOGENESE IN STRELITZIA REGINAE AIT:

Die helmknop van *Strelitzia reginae* is tetrasporangiaat en besit 'n blywende epidermis. Die endotesium ontwikkel veselagtige verdikkings, die middellae gaan verlore en die selle van die klieragtige-tipe tapetum is dikwels tweekernig.

Deling van die mikrospoormoederselle is van die agtereenvolgende tipe en die mikro-

spoortetrades is isobilateraal, T-vorming en lineêr.

Die sferiese stuifmeelkorrels besit gladde wande en is eenkernig wanneer die helmknop oopspring.

INTRODUCTION

Strelitzia reginae Ait. is endemic to South Africa (Phillips, 1951) and is well-known as an ornamental in gardens and parks. The flowers have become very popular in floristry and plants are cultivated for this purpose in many parts of the world. The flower has even been adopted as the civic emblem of Los Angeles.

It is surprising, therefore, that the flowers of this species have rarely been the object of scientific investigation. Apart from the study of Mauritzon (1936) on the embryo-sac development of *S. reginae*, no other work on the embryology of this species could be traced in the literature. Davis (1966) mentions that development of the anther and pollen grains of Strelitziaceae has not been described. In order to gain more information on the embryology of *S. reginae*, a study was made of the microsporogenesis and -gametogenesis of this species.

MATERIAL AND METHODS

Flowers of *S. reginae* were collected from plants growing in Settler's Park, Port Elizabeth. Anthers in different stages of development were fixed and stored in Allen-Bouin type II fluid (Sass, 1958). Dehydration was accomplished in a dioxan-tertiary butyl alcohol series (Sass, 1958) before embedding in wax (Carowax; melting point 54–58°C). Sections were cut on a Jung model 1130 rotary microtome at a thickness of $10 \, \mu \text{m}$. Staining was performed in a Shandon automatic staining machine using the iron-alum-hematoxylin safranin stain of Brooks, Bradley & Anderson (1950). Photographs were taken with a Zeiss photomicrographic camera using Kodak Panatomic X film.

Microspore tetrads were studied by mounting them directly in water, without prior fixation, and viewing under phase contrast. Binucleate microspores were fixed in Carnoy (Sass, 1958), mounted in propionocarmine and viewed under phase contrast.

RESULTS AND DISCUSSION

The anther

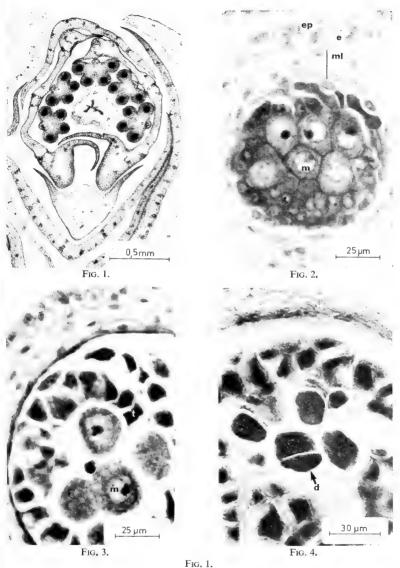
In the flowers of *S. reginae* the margins of two of the petals overlap to enclose five stamens and the style (Fig. 1). The anthers are four-lobed and four-loculed (tetrasporangiate). The lobes remain distinct as the anther matures with the result that the two sporangia on each side of the anther do not become confluent before dehiscence.

The epidermis, or outermost layer of the anther, undergoes anticlinal divisions in order to keep pace with the enlargement of the anther. The compact appearance of these cells is maintained up to maturity, at which time the outer walls are covered by a distinct cuticle.

The young wall of the microsporangium consists of a series of concentric layers of cells (Fig. 2). The outermost of these layers, the endothecium, is situated directly beneath the epidermis. Prior to the release of pollen the cells in this layer develop distinctive fibrous bands of thickenings which stretch from the inner tangential walls to the outer walls.

Adjacent to the endothecium are three to six middle layers. These cells all become flattened and disintegrate as the locules increase in size (see Fig. 3) and have become completely degenerated by the time of dehiscence. According to Davis (1966) this phenomenon is due to the fact that the cells of the middle layers generally lack the ability to divide anticlinally with the result that the tissue cannot adjust itself to the multiplying and expanding sporogenous cells within the sporangium.

The innermost wall layer is the tapetum. In most angiosperms, the tapetum consists of a single layer of cells (Maheshwari, 1950) but in *S. reginae* the microsporocytes are commonly separated from the middle layers by two to three layers of tapetal cells (Fig. 2). The probable role of tapetal cells is that of providing nutrients for the developing spores (Foster & Gifford, 1959). The



Transverse section of a young flower of S. reginae.

Figs. 2-4.

Transverse sections of microsporangia of *S. reginae* (d—dyad, e—endothecium; ep—epidermis of anther, m—microsporocyte, ml—middle layers, t—tapetum).

tapetal cells of *S. reginae* are often binucleate. Davis (1966) mentions that such nuclear divisions are a common feature of tapetal cells.

Just prior to the commencement of meiotic divisions in the microsporocytes, the tapetal cells begin to lose contact with the cells of the middle layers and with one another and are finally absorbed. The tapetum is of the glandular or secretory type. This is the type commonly found in angiosperms (Maheshwari, 1950).

Microsporogenesis

The primary sporogenous cells give rise to the microsporocytes which enlarge until they ultimately have a diameter of 25–30 μ m (Fig. 3). They are easily distinguished from the surrounding tissue because of their large size and prominent nuclei.

Each functional microsporocyte, by means of meiosis and cytokinesis, gives rise to a tetrad of microspores. The divisions of the microspore mother cells are of the successive type, that is, a cell plate is laid down immediately after the first meiotic division (Fig. 4), and another in each of the two daughter cells after the second division. Although there are frequent exceptions, the successive type is prevalent in monocotyledons (Foster & Gifford 1959).

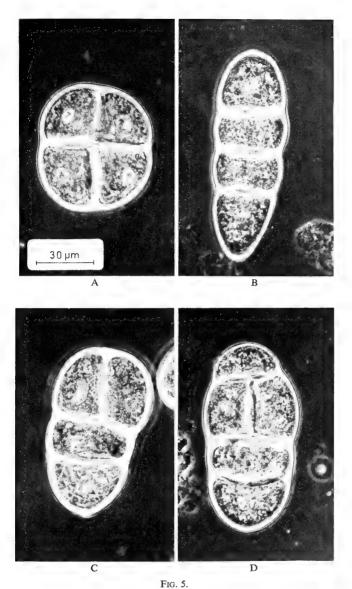
The arrangement of microspores in the tetrads is determined by the orientation of the homeotypic spindles. According to Davis (1966) the arrangement is commonly tetrahedral, isobilateral or decussate. In anthers of *S. reginae* no tetrads were found having the tetrahedral or decussate arrangements. Tetrads having the isobilateral, T-shaped and linear arrangements were found (Fig. 5) and these were present in approximately equal proportions. It is uncommon to find three types of disposition in the same species and the phenomenon has been encountered in species of only a few genera, including *Musa* (Maheshwari, 1950).

Occasionally abnormal tetrads were encountered. Figure 5d pictures such a "tetrad" containing five cells. Groups of as many as eight cells were found in the anthers examined. This phenomenon is known as polyspory and is generally found only in hybrids characterized by a high degree of sterility (Maheshwari, 1950). Pollen grains arising in this way are reported to be nonfunctional.

Microgametogenesis

The spore members of each tetrad soon separate from each other and lie freely within the microsporangium. Each cell rapidly increases in volume and the accompanying vacuolisation is followed by a displacement of the nucleus from the centre to a place adjacent to the wall.

Division of the microspore gives rise to the vegetative and generative cells (Fig. 6). According to Maheshwari (1950) pollen grains are usually either in the



Microspore tetrads of S. reginae

(a) Isobilateral type (b) Linear type (c) T-shaped type (e) Abnormal tetrad containing five spores.

two-celled or three-celled condition when shed, depending on whether the generative cell divides prior to the release of the pollen or not. In the case of *S. reginae*, however, it seems that the vegetative nucleus is short-lived and that it degenerates before the pollen grains reach maturity. All the mature pollen grains examined contained only a single, centrally placed nucleus (Fig. 7). Maheshwari (1950) refers to several species in which the vegetative nucleus is known to degenerate before the pollen grains start to germinate and cites this as evidence against a possible role of this nucleus in directing growth of the pollen tube.

Attempts were made to investigate division of the generative nucleus after germination of the pollen grain. Pollen grains of *S. reginae* can be successfully germinated on an agar medium containing 10 to 15 per cent sucrose, 0,008 per cent boric acid and an aqueous extract of stigma tissue. Various nuclear stains were tested and in all cases the cytoplasm stained intensely and obscured the nuclear material.

The mature pollen grain (Fig. 7) has a dense cytoplasm. It is spherical in shape and has a thick exine and thin intine. The exine is unsculptured and no furrows or pores were observed in this layer. Erdtman (1972) has also observed that the pollen grain of *S. reginae* is nonaperturate.

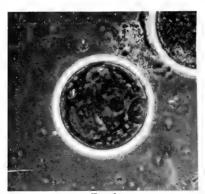
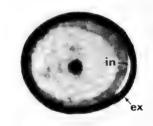


Fig. 6.

Microspore of S. reginae in the two-celled stage.



50 µm

Fig. 7.
Uninucleate pollen grain of S. reginae (ex—exine, in—intine).

ACKNOWLEDGEMENTS

Financial assistance from the Council for Scientific and Industrial Research. as well as the University of Port Elizabeth, is acknowledged.

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DEVELOPMENT AND ACTIVATION OF ORGANELLES IN PROTEA COMPACTA EMBRYOS DURING GERMINATION

J. VAN STADEN AND M. G. GILLILAND (Department of Botany, University of Natal, Pietermaritzburg)

ABSTRACT

The development of glyoxysomes, on which organelle activation in the meristematic roottip of *Protea compacta* embryos depends, appears to be closely connected with the nuclear and membrane state of the cells.

UITTREKSEL

DIE ONTWIKKELING EN AKTIVERING VAN ORGANELLE IN PROTEA COM-PACTA EMBRIOS GEDURENDE ONTKIEMING.

Die ontwikkeling van glioksosome, waarvan die aktivering van organelle in die meristematiese wortelepunt van *Protea compacta* afhanklik is, is waarskynlik nou gebonde aan die staat van die kerne en membrane in die betrokke selle.

Introduction

In an attempt to determine the primary requirements for germination of *Protea compacta* seed it was deemed necessary to investigate the ultrastructural and biochemical changes that occur in these seeds during the germination process. The ultrastructure of dry embryos from both viable and non-viable seed (Van Staden *et al.*, 1975a) and the digestion of food reserves during incubation (Van Staden *et al.*, 1975b) have been reported on. The present paper reports on the development and activation of organelles (or lack thereof) in these embryos.

MATERIAL AND METHODS

Seeds of *Protea compacta* R. Br. were incubated under favourable germination conditions (Brown and Van Staden, 1973) for 20 days. At regular intervals embryos were excised and prepared for electron microscopy as previously described (Van Staden *et al.*, 1975a).

OBSERVATIONS AND DISCUSSION

In the dry state, cells in the meristematic region of the root-tip of viable embryos contained apparently quiescent nuclei. The nucleolus was compact and consisted mainly of fibrillar material. Very little heterochromatin was present in the nucleoplasm. In contrast, nuclei in non-viable embryos contained extensive dense patches of chromatin (Van Staden *et al.*, 1975a). Proplastids,

mitochondria and tubular ER could be observed compressed between the protein and lipid bodies and near the periphery of the cells. Although ribosomes were present in the hyaloplasm it was apparent that protein metabolism and the organelles were in a very low state of activity.

After three days of incubation the nucleolar material in viable embryos increased considerably and became much less compact (Fig. 1). This was accompanied by the appearance of polysomes in the cytoplasm where the ribosomes were arranged in spirals, suggesting the presence of mRNA (Bonnett and Newcomb, 1965) (Fig. 2). During the first five days of incubation only fragments of tubular ER could be observed and mitochondria had few cristae (Fig. 3). Between five and ten days of incubation microbodies with a dense granular content and a single bounding membrane could be seen in intimate association with the lipid bodies. These were identified as glyoxysomes (Van Staden *et al.*, 1975b). After the appearance of these organelles there was a decrease in the number of lipid bodies and starch began to appear in the plastids, which had acquired a rudimentary prolamellar system as a result of budding from the inner membrane of the envelope (Fig. 4). Starch ultimately becomes the main food reserve of these cells.

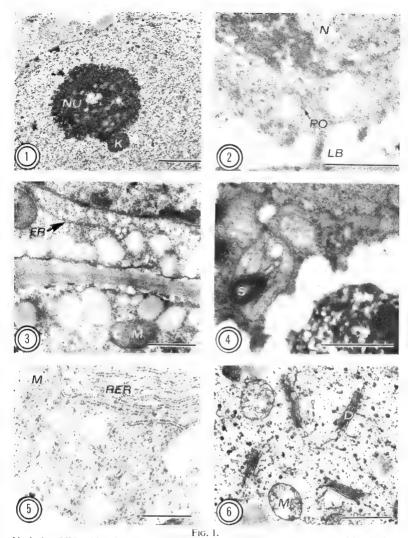
The development of glyoxysomes, which are involved in lipid digestion via the glyoxylate pathway and thus in the generation of energy, is of primary importance for subsequent development of the embryo that ultimately results in radicle elongation. (Van Staden *et al.*, 1975c). In non-viable embryos where this development did not occur no organelle development could be observed.

Following the appearance of glyoxysomes the meristematic cells after 15 days develop an elaborate system of sheet-like rough ER, liberally studded with ribosomes (Fig. 5). Numerous apparently active mitochondria, dictyosomes (Fig. 6) and multi-vesicular bodies also appeared. These latter developments are probably concerned with cell elongation, as the radicles emerge shortly afterwards.

The available evidence suggests that there is some chromosome damage in the necrotic nuclei of the non-viable embryo, which affects the genome and hence protein metabolism (Van Staden *et al.*, 1975a). One of the results of this might be the inability to produce glyoxysomes making it impossible to generate sufficient energy for germination. It has been shown by Villiers (1973) that extensively damaged membrane systems, as occur in non-viable *P. compacta* embryos (Van Staden *et al.*, 1975a), have an inhibitory effect on germination.

ACKNOWLEDGEMENTS

The authors would like to thank the C.S.I.R., Pretoria, for financial support and the EM Unit of the University of Natal, Pietermaritzburg, for technical assistance.



Nucleolus (NU) with a karyosome (K) in a viable root-tip cell after 3 days of incubation. X 16,000. (Bar 2,3 cms = $2 \mu m$).

Fig. 2. Viable embryo cells with polysomes (PO) in the cytoplasm after 5 days of incubation. Configurations suggest the presence of mRNA. X 30,000 (Bar 3 cms = 1 μ m).

Cytoplasm in the radicle meristem after 3 days of imbibition showing fragments of ER and mitochondria with few cristae. X 6,100 (Bar 2 cms = 1 μ m).

Fig. 4. Plastid (P) in a viable embryo with developing starch grain (S) after 10 days of incubation. Small vesicles are budding from the inner membrane. X 30,000 (Bar 3 cms $= 1~\mu m$).

Fig. 5. Rough ER in a meristematic cell of the root-tip of a viable embryo after 10 days of incubation. X 20,000 (Bar 2 cms $= 1~\mu$ m).

Dictyosomes (D) in a meristematic cell of the root tip of a viable embryo after 15 days of incubation. X 20,000 (Bar 2 cms $=1~\mu m$).

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SHORT COMMUNICATION

A NOTE ON OVULAR OUTGROWTHS IN THE SPECIES OF STRELITZIA AIT.

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Seeds of *Strelitzia* species have an appendage in the form of a tuft of bright orange hairs (see Fig. 1) which is commonly called an aril (Wright, 1913; Tomlinson, 1959). Maheshwari (1950) regards an aril as being a third integument; Jackson (1928) gives a similar definition. In *Strelitzia* the outgrowths arise from the funicle on one side of the ovule and from the free end of the outer integument on the other side (Fig. 2) and, consequently, do not constitute a third integument. The appendage can therefore, according to the above definition, not be regarded as an aril.

The ovular outgrowths of *Strelitzia* seem to be similar in origin to the caruncles of *Burbidgea schizocheila* and *Careya arborea* as portrayed by Maheshwari (1950) although, in the text, he defines a caruncle as "a proliferation of the integumentary cells at the micropylar region".

Kapil & Vasil (1963) comment on the vague and indiscriminate use of the term aril by several authors and define the structure as "a secondary collar-like outgrowth which develops from the funiculus and surrounds the ovule more or less completely in post fertilization stages." These authors also regard the appendages of seeds of *Hitchenia caulina*, *Zingiber macrostachyum* and *Elettaria cardamomum*, which are derived partly from the funiculus and partly from the free end of the outer integument, as arils.

In a discussion on ovular outgrowths, Eames (1961) mentions that the use of the terms aril and caruncle is inconsistent. According to this author the term aril is applied rather loosely to fleshy parts of the ovule; to proliferations of the chalaza, the integuments or part of the integuments, to outgrowths of the chalazal region, as well as to fleshy funicles as in *Magnolia* and species of *Acacia*. He concludes that as applied to the angiosperm ovule, aril is obviously merely a descriptive term. If this is the case then the use of the term aril to describe the ovular outgrowths of *Strelitzia* is justified. It does seem, however, that a clear and consistent terminology is required and that a review and classification of ovular outgrowths in general would serve a useful purpose.

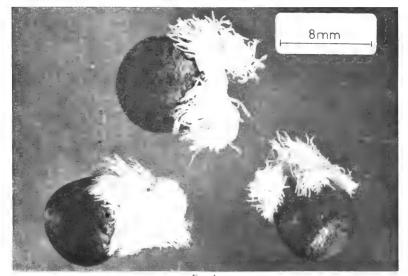
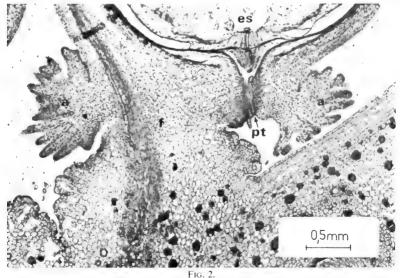


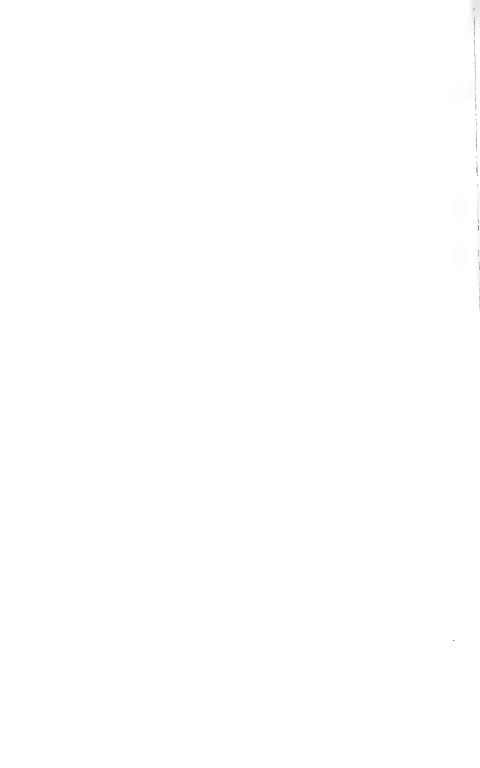
Fig. 1. Seeds of *S. juncea*



Longitudinal section of an ovule of *S. reginae* (a—aril; es—embryosac; f—funicle; pt—pollen tube in micropyle)

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A PORTABLE DRIER FOR HERBARIUM SPECIMENS

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ABSTRACT

A portable oven or drier has been designed for use in the laboratory as well as in the field. Use of this oven saves time and labour and enables one to dry more collected plant specimens in a specified period.

UITTREKSEL

'N DRAAGBARE DROËR VIR HERBARIUMEKSEMPLARE

'n Draagbare droogoond is ontwerp wat in die laboratorium sowel as die veld gebruik kan word. Die gebruik van dié oond bespaar tyd en baie arbeid en maak dit moontlik om in 'n bepaalde tyd meer versamelde plante te droog.

INTRODUCTION

The efficacy of drying herbarium specimens with artificial heat cannot be doubted, although certain workers such as Fernald (1945) according to Lawrence (1963), urge caution in using high temperatures.

When collecting extensively in areas with constant high humidity it is very difficult not to lose a rather large percentage of specimens, due to fungal and bacterial degradation, when the specimens are dried without artificial heat.

A number of drying racks or ovens have been described by McClean and Storey (1930), MacDaniels (1930), Smith (1946) and Lawrence (1963), but none of these are both completely portable and completely efficient.

The drier described here (Fig. 1), has been used under widely divergent field conditions for a number of years and has proved to be very efficient. It has the advantage of being capable of field and herbarium use, depending on either electricity or bottled gas. The mass of the complete drier (except gas cylinder) is less than 13 kg.

For field work the drier folds up into an easily carried package, $58 \times 58 \times 5,5$ cm (Fig. 2), the only loose items being the gas cylinder and lamp head. To assemble takes less than 3 minutes.

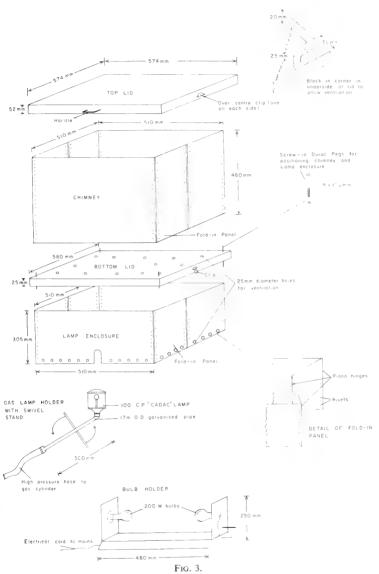
Even plants, resistant to drying, are completely dry within 72 hours, whilst most specimens can be removed from the dryer within 24 hours. This relatively quick drying time, coupled with a capacity of approximately 150 specimens at any one time, allows this drier to be used on extended collecting trips.



Fig. 1. Assembled drier, ready for use.



Fig. 2.
The folded drier is compact and portable.



Exploded diagram, showing construction.

Liquid petroleum gas consumption is approximately 1 kg per 24 hours.

A further advantage is that presses, once packed, do not need to be opened at regular intervals for changing of blotter sheets. Most troublesome insects and mites are also killed or dispelled by the heat.

It is recommended to use corrugated aluminium sheets (450 mm \times 280 mm) as ventilators instead of the usual corrugated cardboard separators in the press.

In the laboratory two 200W bulbs can be used instead of the gas lamp.

Construction (Fig. 3)

The drier consists of a top and bottom lid made of 2 mm aluminium sheet and a chimney and lamp enclosure made of 1,5 mm aluminium sheet.

Wooden blocks in the corners of the top lid provide enough clearance to allow efficient ventilation. No rain, however, can enter the oven and it can therefore be used out of doors.

Dural pegs in the corners of the bottom lid hold the fold-in panels of the chimney and lamp enclosure in position.

For carrying purposes all components are contained in the two lids which fit into one another and are clipped together with two standard overcentre clips.

The holder for the gas lamp is fitted with a swivel stand, enabling it to be carried in the case.

ACKNOWLEDGEMENTS

We would like to thank the instrument makers of the University for advice in designing, and eventually building this oven.

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ON NUMERICAL METHODS FOR CLASSIFYING RELEVÉS COL-LECTED IN BRAUN-BLANQUET PHYTOSOCIOLOGICAL SURVEYS

B. M. CAMPBELL AND E. J. MOLL (Department of Botany, University of Cape Town)

ABSTRACT

The case for using a numerical technique for classifying relevés collected in Braun-Blanquet phytosociological surveys is presented. It is suggested that the method of group-average sorting based on the Canberra similarity measure is a suitable technique. Information loss or distortion is minimal, and the success of the similarity measure is independent of the nature of the raw data. This computer-based method of classifying relevés provides an ecologically interpretable hierarchical classification. Using this classification and a further computer programme for subjectively re-arranging species on the phytosociological table it is possible to effortlessly construct the final table.

UITTREKSEL

NUMERIESE METODES VIR DIE KLASSIFIKASIE VAN RELEVÉS VERSAMEL IN 'N BRAUN-BLANQUET FITOSOSIOLOGIESE OPNAME

Regverdiging vir die gebruik van numeriese tegnieke om die relevés in 'n Braun-Blanquet fitososiologiese opname word aangebied. Dit word voorgestel dat die metode van groepgemiddelde sortering gebasseer op die Canberra gelykvormheidsmaat 'n geskikte tegniek is. Inligtings verlies of verwringing is minimaal en die sukses van die gelykvormigheidsmaat is onafhanklik van die soort onverwerkte data. Hierdie rekenaar-gebasseerde metode om relevés te klassifiseer voorsien 'n ekologiese vertolkbare hiërargiese klassifikasie. Deur hierdie klassifigasie te gebruik asook 'n verdere rekenaarprogram om die soorte subjektiet te herrangskik op die fitososiologiese tabel is dit moontlik om sonder moeite die finale tabel saam te stel.

INTRODUCTION

In Southern Africa the Braun-Blanquet or Zurich-Montpellier method of vegetation survey is becoming increasingly popular (Werger, 1974a). In most surveys the Braun-Blanquet table method (Werger, 1974a; Shimwell, 1971) has been used to construct the final phytosociological table. By this method relevé similarity is visually assessed and the resulting vegetation classification is therefore entirely subjective. Even though the results of this method are often very similar to those obtained by numerical methods (e.g. Spaty et Siegmund, 1973, in Werger, 1974a) this method remains subjective and different workers dealing with the same data are likely to produce different classifications, especially at the lower hierarchical level where there are only subtle differences between relevés and groups of relevés.

This paper is primarily aimed, not at statistical ecologists, but at phytosociologists who wish to obtain numerically-based vegetation classifications. We suggest a numerical method which will provide a classification of relevés for general purposes and which requires no subjective refinement.

DISCUSSION

There are a large number of numerical techniques which could be used to obtain numerically-based vegetation classifications (Williams, 1971) and a number of techniques have been specifically developed for constructing phytosociological tables (Češka and Roemer, 1971; Schmid and Kuhn, 1970 in Werger, 1974a). In two recent papers (Coetzee, 1974; Coetzee and Werger, 1973) the Braun-Blanquet table method was argued to be superior to the numerical methods tested. Both the numerical methods used by these workers have undesirable properties. This is the case with many numerical methods, the efficiency of the method often depending on the nature of the raw data.

In this paper we have considered only those methods which have proved popular or have been developed in South Africa. The method we suggest appears suitable irrespective of the raw data matrix. For accounts of the many methods available reference should be made to Gower (1967), Williams (1971) and Williams, Lance, Webb and Tracey (1973).

Association analysis

One method which should be considered is Association Analysis (Williams and Lambert, 1959; 1961). This method has been widely used in synecological studies (Werger, 1974a) but has had limited success and has, therefore, fallen into general disuse. Failure can be attributed to Association Analysis being a monothetic method, *i.e.* a method in which the groupings in the classification may be defined by a single species. As Coetzee (1974) points out, no species is usually 100% constant in a group of distinctly related relevés, and the chance absence of a defining species from a relevé will result in misclassifications.

If a numerical method is to be useful it should be polythetic, the groupings being based on overall similarity.

Some polythetic methods

Most polythetic methods consist of two steps. The first is the computation of measures of similarity between all relevés to be classified on the basis of their total floristic composition, and secondly the hierarchical arrangement of relevés by sorting through the similarity matrix.

1. Similarity coefficients

The choice of a similarity coefficient requires special consideration of two possible properties of the coefficient (Williams et al., 1973). Firstly, many

coefficients are abundance weighted. The more abundant species may, therefore, dominate the analysis and potential information from less abundant species may be lost. Such coefficients are undesirable as they require an intuitive assessment of the data prior to analysis as standardisation may be necessary to ensure the success of the coefficient; for example square-root or logarithmic transformation (Field, 1971; Walker, 1974).

However, abundance-weighted coefficients appear not too problematical with Braun-Blanquet phytosociological data, as the cover-abundance values are semi-logarithmically transformed relative to the actual cover. For example species with 76 to 100% cover having a cover-abundance value of 5 while species with 1 to 5% cover being considered only 5 × less 'important', i.e. having a value of 1. For this reason the results of a classification using the abundance-weighted Bray and Curtis measure* are almost identical to that given by the Canberra measure which is not abundance weighted (Fig. 1.). The groups recognised in the classifications are easily ecologically explainable.† Although the Bray and Curtis measure has proved successful, its abundance weighting property will be undesirable for some data matrices. The Euclidean metric is excessively sensitive to relative abundance (Williams et al., 1973) and its success is, therefore, dependent on the nature of the raw data.

The second property which requires consideration is whether the similarity measure excludes double zero matches, *i.e.* joint absences of given species. That these matches are excluded is desirable for, as Field (1969) suggests, 'no marine ecologist would consider that the intertidal and abyssal faunas were similar because both lacked the species found on the continental shelf'. Measures which include double zero matches are, therefore, of restricted use, their success depending on the nature of the raw data. They will only be successful with raw data in which there are few zero values. Measures of this type include most information statistics (*i.e.* information analysis of Williams, Lambert and Lance, 1966) and the product moment correlation (as used by Coetzee

$$C = \frac{2w}{A+B} \times 100$$

where w is the sum of the lesser values of the species scores in the two plots compared; A and B are the sums of the species scores in each plot; C is the percentage similarity between the plots.

^{*} The Bray and Curtis measure or Czekanowski coefficient or Sorenson coefficient (Bray and Curtis, 1957; Field, 1971; Williams et al, 1973) is:

[†] The data used in Figs. 1 and 2 are from Campbell (1974) and consist of 39 relevés with 65 species. The relevés were collected from forest patches on the Cape Peninsula. The degree of inter-relevé variability or heterogeneity in the data was low; approximately 20% of the values in the data matrix being zero.

et al., 1973). This latter coefficient also suffers from another problem; its sensitivity to the departure of a species abundance value from the mean value in a plot (Hall, 1969).

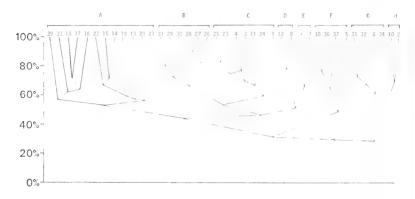


Fig. 1a.

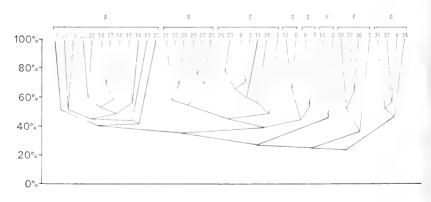


Fig. 1b.

Comparison of the group average relationships (see text) of forest relevés collected by Campbell (1974) as given by (a) the abundance weighted Bray and Curtis measure and (b) Canberra measure which is not abundance weighted. The letters A-H indicate the groups recognised.

The scale shows percentage similarity.

The frequency modulated relative homogeneity function (Hqm) of Hall (1969) was also considered. Using this function weighting of species abundance values can be varied by the investigator. When no weighting is used double zero matches affect the analysis. No weighting is therefore unsuccessful when there are a large number of zero values in the data matrix, as is shown in the test data (Table 1). Seventy percent of the values in this matrix are zero values. The degree of inter-relevé variability or heterogeneity in the data is, therefore, high.

TABLE 1.
Test Data

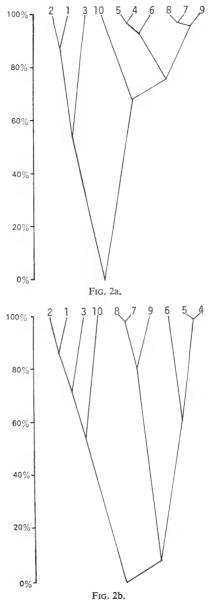
	plot numbers										
	1	2	3	4	5	6	7	8	9	10	
1	5	3	5					-			
2	2	2	1	_	-	-	-	-	-	-	
3	1	1	-	-	-	-	-	-	-	-	
4	_	1	2	-	-	_	_	_	_	-	
5	1	1	_	-	-	-	-	-	-	-	
6	-	-	-	5	5	3	_	1		_	
7	-	-	_	_	1	-	5	5	4	_	
8	5	5	5	-	-	-	-	-	-	5	
8	3	3	3	-	_	-	_	-	_	-	

species numbers

The classification of these data by Hqm (Fig. 2) shows that it is necessary to use Hqm fully abundance weighted if plot 10, which actually shows no similarity to plots 4, 5, 6, 7, 8 and 9, is not to be grouped with these plots. However, in other situations no abundance weighting may prove more successful than full abundance weighting. This can occur when the data matrix has few zero values, as was the case in the forest data used to construct Fig. 1. Here abundance weighting provided a classification that was difficult to interpret whereas Hqm, with no abundance weighting, provided a classification similar to those produced by the Canberra measure and Bray and Curtis measure (Fig. 3).* Hqm must therefore be discarded as a possible standard all-purpose similarity measure; its efficiency being dependent on the investigator's

^{*} For sorting the similarity values obtained from the Canberra measure and Bray and Curtis measure the method of group-average sorting was used (see following discussion), while the method of average member sorting of Hall (1969) was used with Hqm. The two different sorting methods could not explain the differences in the dendrograms as the methods are similar; average member sorting having a minimally better averaging technique (Hall, 1969; Field, 1971). However, this method requires much more computation time.

subjective assessment of the data and his subsequent choice of abundance weighting.



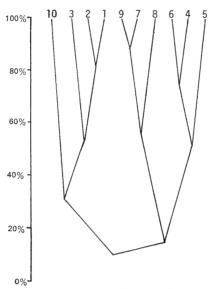
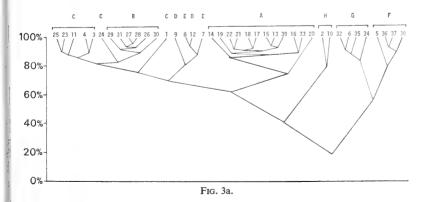
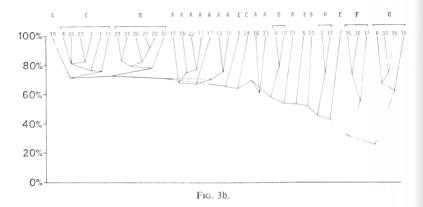


Fig. 2c.

Classifications of a raw data matrix with many zeros (Table 1) using (a) Hqm with 0% abundance weighting (b) Hqm with 100% abundance weighting and (c) the Canberra measure which excludes double zero matches. Plot 10 is misclassified in the first dendrogram.





Classifications of the forest data used for Fig. 1 (Campbell, 1974) using (a) Hqm with 0% abundance weighting and (b) Hqm with 100% abundance weighting. As opposed to Fig. 2 Hqm with 0% abundance weighting now provides more acceptable groupings. A-H indicate the groups that were recognised in Fig. 1.

One measure which would appear suitable is the Canberra measure.

$$C = \frac{1}{s} \frac{\Sigma}{j} \left\{ \frac{\textbf{I} \textbf{x}_{1j} - \textbf{x}_{2j} \textbf{I}}{\textbf{x}_{1j} + \textbf{x}_{2j}} \right\} \times 100$$

where x_1 is the abundance value of the jth species in plot 1; s is the total non double-zero matches of the species in the plots being compared, and C is the percentage dissimilarity of the plots. It has a slight problem in that when x_{1j} is zero the measure takes on its maximum value irrespective of the value of x_{2i} . This can be overcome by replacing zero by a small positive value for all zero/non-zero comparisons e.g. 0,1 (Williams et al., 1973). This measure, being self-standardising over each comparison, is quite insensitive to large outlying values. It also does not consider double-zero matches (cf Fig. 2c). It would therefore appear to be of use as a similarity measure which can accept raw data which does not require manipulation prior to analysis; its success being independent of the nature of the raw data. It has produced favourable results in the work of Williams et al. (1973) and Webb, Tracey, Williams and Lance (1970), and also in forest and fynbos vegetation that the present authors are studying.

2. Sorting (Cluster) technique

The method of group-average sorting would appear to be suitable as a standard method for sorting or clustering items and groups of items. In studies by the present authors and by Field (1970, 1971) this method has proved successful. Hall (1969) mentions that information loss by this method is minimal. In this sorting method the most similar plots are grouped. The similarity coefficients between each plot of a newly formed group and a plot outside the group are then averaged. This is done for every plot outside a group to give new similarity coefficients between the group and the rest of the plots, so that in further groupings, the already formed groups are regarded as single plots.

Computation aspects

The time and effort required to prepare the raw data for computation may be cited as a problem in numerical analyses. However, in terms of time, the present authors have shown that to prepare a final Braun-Blanquet phytosociological table requires more time when manually prepared than when prepared with computer-based aids. We have prepared final phytosociological tables by using the vegetation classification as given by the Canberra measure and group-average sorting using a programme written by Dr. J. Field* and modified by B.C. Classification of species using the above technique has been unsuccessful. In tables completed to date the species have been subjectively arranged using a computer-based technique. As compared to manual methods of preparing phytosociological tables, both by rewriting and mechanical aids, the computer-based method has proved less time consuming and laborious, and is not a potential source of error. The data prepared for computation are then also available for analysis by a variety of numerical methods (e.g. ordination).

One serious problem with a computer-based method is the limitation on the size of the raw data matrix. This can however be overcome by methods such as those proposed by Janssen (1975). The essence of Janssen's method is that each relevé is considered separately, and only in relation to the relevés considered before. Clusters are formed through either assigning a new relevé to an already existing cluster, or to designate it as a separate cluster. In this way relevés can be divided into a number of clusters each of which can then be used in more detailed analyses.

CONCLUSIONS

Werger's (1974b) suggestion that the classification arrived at by numerical methods is not necessarily versatile, does not fully apply to the above technique.

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Forest data collected by Campbell (1974) were used to construct the dendrogram shown in Fig. 1. At a later date 66 further plots were collected from the forests under study and together with the initial plots were numerically analysed. The new data matrix now consisted of 105 plots with 120 species and a slightly higher inter-relevé variability; approximately 45° of the values being zero values. The resulting classification (Fig. 4) shows that the groupings obtained still hold in the final classification; except for plot 1 which, however, was the most atypical plot of group C. The method would therefore appear to be relatively versatile.

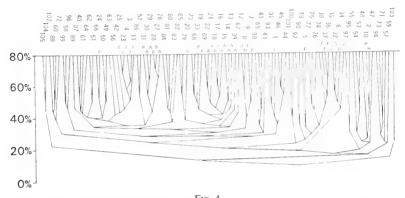


Fig. 4.

Group-average relationships of 105 forest relevés using the Canberra measure. Plots 1-39 were used in Fig. 1. A-H indicate the groups in which these plots were found in Fig. 1.

If a standard numerical method is available to classify relevés, the following benefits to phytosociologists can be envisaged:

- 1. a high reliability can be placed on the vegetation classifications obtained by different workers in different areas;
- standardisation by different workers allows ease of comparison between workers;
- 3. a numerical method can provide an objective means of delineating syntaxa at the lower hierarchical levels where the differences between taxa are slight. This has been shown in our work on the Cape Peninsula where it has been possible to subdivide a large number of relevés with very similar floristics;
- the classification which results can be expressed as a dendrogram which provides a clear graphical method of showing the similarity between relevés and groups of relevés;

5. an eventual aim of phytosociologists should be an inventory of the plant communities of South Africa. Computer-based methods are essential for this mammoth task. This aim will be made that much more attainable if the data are available in a machine readable form. Using a numerical method, quantitative values can be used to indicate syntaxonomical rank, e.g. 20–30% similarity may indicate the association level.

These benefits can only be realised if one of the number of equally recommended methods can be found suitable. The suggested method must avoid information loss and distortion and must provide a classification for general purposes. The results of the method should not depend on the nature of the raw matrix (i.e. raw table). As Goodall (1970) has stated, it is doubtful whether any single method will be consistently preferable. Different methods will stress different facets of the data. Nevertheless, group-average sorting based on similarity values obtained by the Canberra measure appears to be highly suitable as a general method of classifying relevés.

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THE STRUCTURE AND ONTOGENY OF THE CHLORENCHYMA IN THE STEMS OF ELEGIA L. (RESTIONACEAE)*

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ABSTRACT

The leaves (leaf sheaths) of the thirty-seven *Elegia* species studied are sessile, much reduced, often deciduous and in most cases without chlorenchyma.

In the stems however, a chlorenchymatous tissue is found on the inner side of a multiseriate

epidermis.

The chlorenchyma consists of two types of cells namely protective cells and peg cells. These cells differentiate from the outer part of the ground meristem.

UITTREKSEL

DIE STRUKTUUR EN ONTOGENIE VAN DIE CHLORENCHIEM IN DIE STINGELS VAN ELEGIA L. (RESTIONACEAE)

Die blare (blaarskedes) van die sewe en dertig *Elegia*-spesies wat bestudeer is, is sittend, baie gereduseerd, dikwels afvallend en gewoonlik sonder enige chlorenchiem.

In die stingels kom daar egter 'n goed ontwikkelde chlorenchiemweefsel aan die binnekant

van 'n meerlagige epidermis voor.

Die chlorenchiem bestaan uit twee seltipes nl. voeringselle (protective cells) en balkselle (peg cells). Hierdie selle differensieer uit die buitenste gedeelte van die grondmeristeem.

Introduction

Elegia L. (Restionaceae) is a xerophytic, perennial, dioecious, herbaceous monocotyledonous genus. It is endemic to South Africa and its natural occurrence is restricted to the southern and south-western parts of the Cape Province.

The orthotropic, aerial stems of the different species vary in length from 200 mm to 2 m. The stems of some species are branched while in others they are unbranched. In two species the branches are arranged in whorls.

The leaves are sessile and with exception of the bracts in the inflorescence, often deciduous. Although the leaf colour of a species is fairly constant, it varies from dark brown to yellow in different species. These anomalous leaf colours are due to the poor development (or absence) of chlorenchymatous tissue.

Based on a thesis, submitted by the first author to the University of Pretoria in partial fulfilment for the M.Sc. degree.

Accepted for publication 20th August, 1975.

MATERIAL AND METHODS

The anatomy of the median parts of the stem internodes of thirty-seven different species was comparatively studied. For ontogenetic studies, apical and intercalary meristems of young stems of *E. vaginulata* Mast. were used.

Collected fresh material was immediately fixed in F.A.A. (formalin-acetic acid-alcohol), dehydrated with TBA (tertiary butanol) and embedded in "Tissue-Mat" wax. Sections of apical and intercalary meristems were cut at 8 μ m. All other sections were cut at 10 μ m. All sections for light microscopic work were stained with haematoxylin/safranin (Johansen, 1940). Unstained sections for the scanning electron microscope were mounted on part of a microscope glass cover slip and vacuum coated with gold/palladium.

RESULTS AND DISCUSSION

The two to three layered chlorenchyma is located directly under the epidermis and consists of two different cell types viz. protective and peg cells (Cutler, 1969) (Fig. 1).

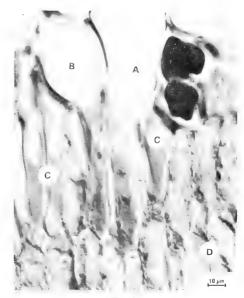


Fig. 1.

Cross-section through the epidermis and chlorenchyma in the stem of *E. vaginulata* Mast. A, substomatal chamber; B, epidermis cell; C, protective cells; D, peg cells.

Peg Cells

The outer two layers of the parenchyma, containing numerous chloroplasts, consist of radially elongated cells all of approximately the same length. The cells of the third layer vary from irregular to spherical in shape. Very few chloroplasts are visible in these cells. Nuclei are clearly visible.

Intercellular spaces occur between the radial, transversal and slanting tangential walls of the adjacent cells.

Numerous pegs (Fig. 2) connect adjacent peg cells with one another. Peg cells are also connected with protective cells by means of these pegs.

Scanning electron micrographs show no pits or pores associated with the peg connections between the peg cells (Fig. 2).

Although pegs are typical of the abovementioned cell walls they were not observed on any of the tangential walls between epidermis and chlorenchyma, nor could they be found between the chlorenchyma and the parenchyma sheath to the inner side of the chlorenchyma.

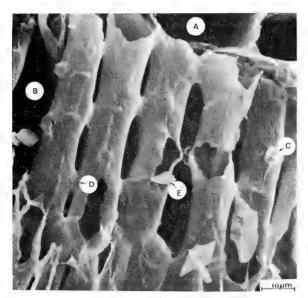


Fig. 2.

Scanning electron micrograph of peg cells and epidermis in the stem of *E. vaginulata* Mast. A, epidermis; B, intercellular space; C, vertical view of peg; D, peg as seen from the side; E, ruptured cell wall of peg cell.

Protective Cells

The use of the term protective cells (Cutler, 1969) is based on the assumption that these cells have a protective function since the walls lining the substomatal chamber have a thin cuticle.

Athough this name is accepted by the authors, it must be stressed that no experimental data exist to confirm this hypothesis. Protective cells are apparently always associated with stomata. Together with cells of the inner epidermis, they form a lining for the substomatal chamber. In median transections of the stomata, protective cells on opposite sides of the substomatal chamber are attached to each other at their bases only.

Protective cells are radially elongated with lignified cell walls and are usually longer than the peg cells, reaching up to half way or even further down into the second peg cell layer. No chloroplasts or nuclei were observed in these cells.

Ontogeny

Although the histogens—protoderm, ground meristem and procambium—differentiate from the intercalary meristem at the base of the second internode, the differentiation of the various tissues only commences in the fifth internode.

The chlorenchyma is the first tissue to differentiate from the ground meristem and occurs at the outer side of the ground meristem directly underneath the protoderm/epidermis.

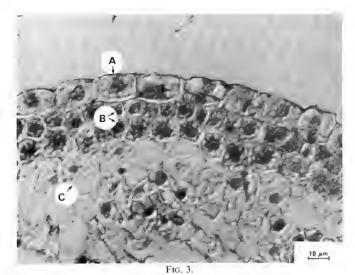
At this stage the cells of the chlorenchyma are arranged in two layers and are polygonal and approximately uniform in size. The cell contents stain intensely. Intercellular spaces do not occur yet. No distinction can be made between the precursors of the peg cells and protective cells (Fig. 3).

Chloroplasts can easily be observed in these cells.

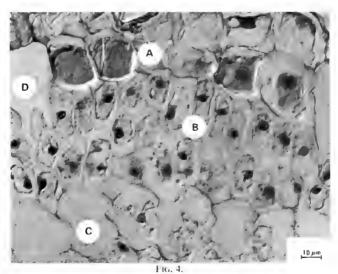
During growth and development of the stem, the outer circumference of the chlorenchyma increased with 45%.

The total width of the stretched individual cells however, accounts only for 34% of this increase in circumference. This is due to the fact that radial cell elongation exceeds tangential cell elongation, (compare Figs. 3, 4 and 5). The remaining 11% increase of the circumference is due to newly formed intercellular spaces and substomatal chambers.

As a result of incomplete schizogeny, these intercellular spaces do not occur over the whole length of the radial cell walls. The areas where intercellular spaces are not formed, and where the adjacent cell walls adhere locally to one another, constitute the pegs which are visible at a later stage of development. The protective cells have a greater radial elongation rate than the peg cells and differentiate later than the peg cells together with the substomatal chambers (compare Figs. 3 and 4).



Embryonic tissues in the stem of E. vaginulata Mast. A, protoderm; B, chlorenchyma; C, parenchyma sheath.



Immature tissues in the stem of *E. vaginulata* Mast. A, epidermis; B, chlorenchyma; C, parenchyma sheath; D, substomatal chamber.

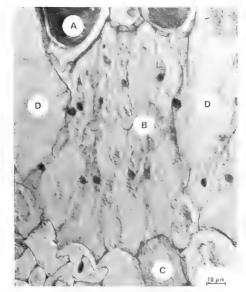


Fig. 5.

Immature tissues in the stem of *E. vaginulata* Mast. at a later stage of development than in fig. 4. A, epidermis; B, chlorenchyma; C, parenchyma sheath; D, substomatal chamber.

CONCLUSION

The chlorenchyma in the stem of *Elegia* L. is a specialized tissue with characteristic structure. This ontogenetic study revealed the origin of this highly modified parenchyma tissue and its differentiation into peg cells and protective cells.

ACKNOWLEDGEMENTS

We wish to thank the Research Committee of the University of Pretoria and the C.S.I.R. for financial aid. A special word of thanks to Miss E. Esterhuysen of the Bolus Herbarium for her help in the collection and identification of material.

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NOTES ON THE MORPHOLOGY OF THE EMBRYO AND SEEDLING OF STRELITZIA REGINAE AIT.

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ABSTRACT

The embryo of *S. reginae* is an elongated, club-shaped organ, the bulk of which consists of a massive cotyledon. Germination is hypogeal. The apex of the cotyledon, corresponding to the leaf blade, remains in the seed during germination and functions as a haustorium. Elongation growth of the basal portion of the cotyledon carries the plant axis into the soil. A short cotyledonary petiole separates the plant axis from the haustorium.

Proliferation of cells around the cotyledonary cleft results in the formation of a ligule while extensive elongation of the basal portion of the cotyledonary sheath is absent.

The first leaf to emerge from the ligule is a tubular scale leaf while the second leaf to appear is the first laminate leaf.

UITTREKSEL

AANTEKENINGE OOR DIE MORFOLOGIE VAN DIE EMBRIO EN SAAILING VAN STRELITZIA REGINAE AIT.

Die embrio van S. reginae is 'n verlengde, knuppelvormige orgaan waarvan die grootste gedeelte uit die saadlob bestaan. Ontkieming is hipogeaal. Die apikale gedeelte van die saadlob, wat ooreenstem met die blaarskyf, bly in die saad gedurende ontkieming en funksioneer as 'n houstorium. Verlenging van die basale gedeelte van die saadlob dra die plantas in die grond in. 'n Kort saadlobpetiolus skei die plantas van die houstorium.

Proliferasie van selle rondom die saadlobspleet lei tot die vorming van 'n liguul terwyl

uitgebreide verlenging van die saadlobskede self, afwesig is.

Die eerste blaar wat deur die liguul verskyn is 'n buisagtige skubblaar terwyl die tweede blaar die eerste is wat 'n blaarskyf besit.

INTRODUCTION

Aspects of the embryology of *S. reginae* have been investigated by Mauritzon (1936) and van de Venter (1975) while the anatomy of the seed has been described by Humphrey (1896). The embryogeny of this species has not been described, nor has a description been given of the morphology of germinating seeds.

This paper reports on an investigation into the morphology of the mature embryo and the young seedling.

MATERIAL AND METHODS

Embryos and seedlings of *S. reginae* were fixed in Craf II solution (Sass, 1958). Dehydration was accomplished in a dioxan-tertiary butyl alcohol series (Sass, 1958) before embedding in wax (Carowax; melting point 54–58°C).

Sections were cut on a Jung model 1130 rotary microtome at a thickness of $10~\mu m$. Sections were stained with the iron-alum-hematoxylin safranin stain of Brooks, Bradley & Anderson (1950) and photographs taken with a Zeiss photomicrographic camera using Kodak Panatomic X film.

RESULTS AND DISCUSSION

In the "ripe" or mature seed of *S. reginae* the embryo lies within a cavity in the endosperm (Fig. 1). The embryo is not attached to any part of the seed structure and can be removed simply by cutting through the surrounding tissue and splitting the seed in half.

The embryo is an elongated, club-shaped organ which, after imbibition, is more or less circular in transverse section. It is about 7 mm long and extends from the micropyle to a point approximately 0,6 mm below the testa on the opposite side of the seed.

The bulk of the embryo consists of the massive cotyledon. The portion corresponding to the leaf blade is separated from the basal portion of the embryo, which contains the radicle and plumule, by a slight constriction. The former portion remains in the seed during germination and serves as a haustorium. The different parts of the embryo are shown in Fig. 2. Several procambial strands extend from the basal portion to the apex of the embryo.

The basal portion of the embryo contains the plumular bud and radicle. The plumular bud is surrounded by the cotyledonary sheath which, as can be seen in a transverse section (Fig. 3), contains a narrow cleft. This cleft is formed as a result of the narrowing down of the cotyledonary indentation in the developing embryo (Fig. 4) by the growth of the surrounding tissue.

The radicle apex lacks a clear differentiation of initials (Fig. 5). This is classed as the open type of organization (Von Guttenberg, 1960) in which the tissue regions (central cylinder, cortex, root cap and protoderm) merge in a common group of initial cells (i in Fig. 5). A prominent root cap overlies the radicle.

The embryo requires no further differentiation or growth as a prerequisite for germination as has been demonstrated by the fact that isolated embryos grow promptly when placed in a suitable medium (van de Venter & Small, 1974).

With the commencement of germination a zone of cotyledonary tissue between the sheathing base and haustorium elongates resulting in the rupture of the testa. As a result of this extension growth the primary seedling axis is carried out of the seed into the soil.

The primary root with its prominent root cap is the first portion of the embryo to emerge. In the mature embryo the epidermis of the root cap, and not the protoderm of the young radicle, is continuous with the epidermis of the cotyledon (Fig. 5). The result is that extension growth of the radicle ruptures

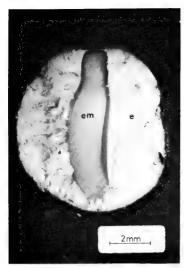
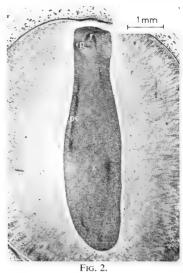


FIG. 1.

Imbibed seed of *S. reginae* split in half to show embryo; e—endosperm).



Longitudinal section of a mature embryo of S. reginae (c—cotyledon; pc—procambium; p—plumular bud; r—radicle).

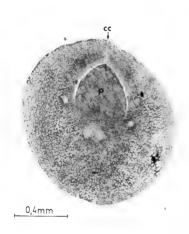


Fig. 3.

Transverse section of an embryo of *S. reginae* at the level of the plumular bud. (cc—cotyledonary cleft; p—plumular bud).

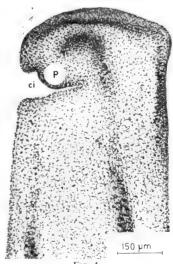


Fig. 4.

Longitudinal section of a developing embryo of *S. reginae* (ci—cotyledonary indentation; p—developing plumule).

the epidermis of the embryo (see arrows in Fig. 6) and the epidermis of the primary root is not continuous with that of the rest of the seedling.

Germination is hypogeal. The mode of germination corresponds to the type C in the classification of Boyd (1932). The following description assumes that the long axis of the embryo is aligned parallel to the soil surface before germination commences. At first the axis of the embryo emerging from the seed is not directed vertically downwards, but at an obtuse angle to the axis of the haustorium. In their final orientation, however, the plumular bud and the radicle are in a vertical alignment at right angles to the cotyledon haustorium. The seedling axis is separated from the haustorium by a short (about 2 mm in length) stalk or cotyledonary petiole (Fig. 7).

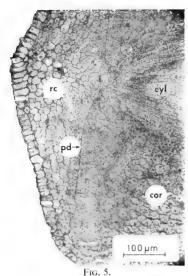
The basal portion of the cotyledonary sheath does not elongate to form a prominent sheathing organ, as is the case with some monocotyledonous species (Tomlinson, 1960). However, proliferation of cotyledonary sheath tissue on the margins of the cotyledonary cleft results in the formation of a ligule (Figs. 7 and 8). Boyd (1932) regards production of a ligule coupled with the disappearance of the lower sheath to be an advanced characteristic.

The first foliar organ to be produced from the plumular bud appears through a small pore at the apex of the developing ligule when the primary root has attained a length of about 8 mm (Fig. 7). The first leaf to emerge is a scale leaf—a tubular, sheathing organ. The second leaf is the first laminate leaf.

The part of the cotyledon corresponding to the leaf blade remains permanently in the seed and functions as a suctorial structure. The endosperm cells are filled with amyloplasts (Fig. 9) and the starch in these organelles is, no doubt, broken down and absorbed by the haustorium with subsequent transport to the developing seedling. Apart from the increase in volume as a result of imbibition, the cotyledon does not change in shape during or subsequent to germination, nor do any special epidermal modifications differentiate. Such changes occur in the cotyledons of many monocotyledonous species (Eames, 1961).

Anatomical changes do however, take place in the haustorium after commencement of germination. The procambium strands differentiate into vascular tissue (Fig. 10). The number of vascular bundles per cotyledon is not constant but varies from seven to eleven. The xylem is situated on the inner side of each vascular bundle, that is, it is directed toward the central axis of the cotyledon. Scalariform and pitted vessels are shown in Fig. 11. An abundance of phloem tissue is differentiated on the outer side of the vascular bundles.

The primordium of the first adventitious root is visible (upon sectioning) before the first leaf emerges from the ligule. By the time the third laminate leaf appears, the first adventitious root is as long as the primary root (about 10 cm). When the sixth laminate leaf becomes visible, the root system consists of three to five prominent, fleshy adventitious roots.



Longitudinal section of a radicle of an embryo of *S. regimae* (cor—cortex; cyl—central cylinder; i—initial cells; pd—protoderm; rc—root cap).



Longitudinal section of the plant axis of S. reginae shortly after germination. (p—plumule; r—radicle).

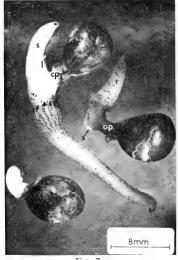
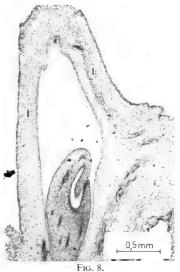
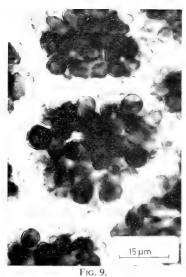


Fig. 7.

Germinating *S. reginae* seeds. (cp—cotyledonary petiole; l—ligule; r—radicle; s—scale leaf).



Longitudinal section of plumule and ligule of a *S. reginae* seedling. (l—ligule).



Section of endosperm cells in a seed of S. reginae showing amyloplasts stained with I_2KI .

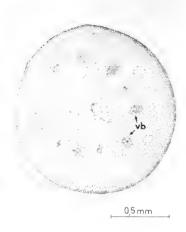
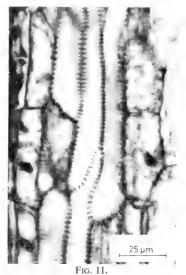


Fig. 10.

Transverse section of the haustorium in a germinated seed of *S. reginae* (vb—vascular bundles).



Longitudinal section of the xylem in a haustorium of a germinated seed of S. reginae.

ACKNOWLEDGEMENTS

Financial assistance from the Council for Scientific and Industrial Research is acknowledged.

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STUDIES IN THE XYLARIACEAE: SUPPLEMENTARY NOTE.

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At the time of publication of the series "Studies in the Xylariaceae (Journal of South African Botany 33: 315–328, 1967; 34: 153–199, 1968; 34: 303–330, 1968; 35: 149–206, 1969; 35: 267–320, 1969; 35: 393–410, 1969; 36: 73–138, 1970) insufficient information was available about many of the basionyms and first publications of many of the species transferred from one genus to another. Following is a list of basionyms for the new combinations and species proposed, prepared with the help of Dr. B. C. Sutton and Mrs. B. Thomas of the Commonwealth Mycological Institute, Kew.

NEW COMBINATIONS WITH BASIONYMS

- 1. Anthostomella flavoviridis (Ell. & Holw.) Martin Basionym: *Anthostoma flavoviride* Ellis & Holway apud Arth. et al., in Bull. Minn. Geol. & Nat. Hist. Surv., bot. Ser. 3, p. 32, 1887. (Fide E. Cash, *Record of the Fungi named by J. B. Ellis*).
- Anthostomella italica (Sacc. & Speg.) Martin
 Basionym: Anthostoma italicum Saccardo & Spegazzini in Michelia 1,
 1:326, 1878.
- 3. Anthostomella melanotes (Berk. & Br.) Martin Basionym: *Sphaeria melanotes* Berkeley & Broome in Ann. Mag. nat. Hist. Ser. 2, 9:321, (No. 623), 1852.
- 4. Anthostomella sustenta (Plowr.) Martin Basionym: Sphaeria sustenta Plowright in Grevillea 7: 73, 1878.
- 5. Anthostomella uda (Pers. ex Fr.) Martin Basionym: Sphaeria uda Persoon ex Fries, Syst. mycol. 2: 358, 1823.
- Anthostomella xylostei (Pers. ex Fr.) Martin Basionym: Sphaeria xylostei Pers. ex Fries, Syst. mycol. 2: 487, 1823. Syn: Anthostoma xylostei (Pers. ex Fr.) Saccardo, (1878).
- Hypoxylon acuminosporum Martin, nom. nov. Basionym: Rosellinia merrillii Sydow in Philipp. J. Sci. 8: 485, 1913. (Non Hypoxylon merrillii Syd. 8, 1917).

- 8. Hypoxylon albolanatum (Ell. & Everh.) Martin
 - Basionym: Rosellinia albolanata Ellis & Everhart in Proc. Acad. nat. Sci. Phila. 1890: 227, 1890.
- 9. Hypoxylon apiculatum (Sacc.) Martin
 - Basionym: Rosellinia apiculata Saccardo in Michelia 1: 26, 1877.
- 10. Hypoxylon asperatum (Massee) Martin
 - Basionym: Rosellinia asperata Massee apud Wakefield in Kew Bull. 1: 209, 1918.
- 11. **Hypoxylon bermudense** (Miller) Martin (N.B. neuter epithet ending) Basionym: *Penzigia bermudensis* J. H. Miller in Mycologia **32:** 402, 1940.
- Hypoxylon bicoloratum Martin, nom. nov.
 Basionym: Hypoxylon bicolor Ellis & Everhart in J. Mycol. 2: 88, 1886.
 (Non Hypoxylon bicolor Berk. & Curt.).
- 13. **Hypoxylon bresadolae** (Theissen) Martin
 - Basionym: Rosellinia bresadolae Theissen in Annls mycol. 6: 351, 1908.
- Hypoxylon bunodes (Berk. & Br.) Martin
 Basionym: Sphaeria bunodes in J. Linn. Soc., Lond. bot. 14: 125, 1873.
- 15. **Hypoxylon buxi** (Fabre) Martin
 - Basionym: Rosellinia buxi Fabre in Ann. Sci. nat. Ser. 6, 9: 78, 1878.
- Hypoxylon callimorphum (Karst.) Martin Basionym: Rosellinia callimorpha Karsten in Hedwigia 23: 84, 1884.
- Hypoxylon geasteroides (Ellis & Everhart) Martin Basionym: Rosellinia geasteroides Ellis & Everhart in Proc. Acad. nat. Sci. Philad. 1895: 415, 1895.
- 18. **Hypoxylon giganteum** (E. & E.) Martin Basionym: *Rosellinia gigantea* Ellis & Everhart apud C. L. Smith in Bull. Iowa Univ. Lab. Nat. Hist. **2:** p. 401, 1893.
- 19. **Hypoxylon gigasporum** (E. & E.) Martin Basionym: *Rosellinia gigasporum* Ellis & Everhart apud C. L. Smith in Bull. Iowa Univ. Lab. Nat. Hist. **2:** p. 401, 1893.
- 20. **Hypoxylon griseocinctum** (Starb.) Martin Basionym: *Rosellinia griseocincta* Starback in Bih. K. Svensk. Vet.-Akad. Handl. **25** (3), Afd. 3, No. 1: p. 49, 1899.
- Hypoxylon herpotrichioides (Hept. & Dav.) Martin Basionym: Rosellinia herpotrichioides Hepting & Davidson in Phytopathology 27: 307, 1937.
- Hypoxylon julii (Fabre) Martin
 Basionym: Rosellinia julii Fabre in Ann. Sci. Nat. Ser. 6, 9: 79, 1878.
- Hypoxylon lamprostomum (Syd.) Martin Basionym: Rosellinia lamprostoma Sydow in Philippine J. Sci. 8: 273, 1913.

24. Hypoxylon langloisii (Ell. & Everh.) Martin

Basionym: Rosellinia langloisii Ellis & Everhart in Proc. Acad. nat. Sci. Philad. 1890: 228, 1890.

25. Hypoxylon limoniisporum (Ell. & Everh.) Martin

Rosellinia limoniispora Ellis & Everhart in Proc. Acad. nat. Sci. Philad. 1894; 326, 1894.

26. Hypoxylon mammiformie (Pers. ex Fr.) Martin

Basionym: Sphaeria mammiformis (as 'mammaeformis') Persoon ex Fries, Syst. mycol. 2: 455, 1823.

Hypoxylon medullare (Wallr.) Martin (N.B. neuter epithet ending) Basionym: Sphaeria medullaris Wallroth, Flora crypt. Ger. p. 792, 1833.

28. Hypoxylon megalocarpum (Plow.) Martin

Basionym: Sphaeria megalocarpa Plowright in Grevillea 7: 73, 1878.

29. Hypoxylon megalospermum (Syd.) Martin

Basionym: Rosellinia megalosperma Sydow in Philipp. J. Sci. 8: 485, 1913.

30. Hypoxylon mutans (Cooke & Peck) Martin

Basionym: Sphaeria mutans Cooke & Peck apud Peck in 29th Report N.Y. St. Bot. 1875, p. 64, 1878.

31. Hypoxylon necatrix (Hart.) Martin

Basionym: Rhizomorpha necatrix R. Hartig in Unters. forstbot. Inst., Munchen 3, p. 95, 1883. (Reference not seen here, but probably alright.)

32. Hypoxylon perfidiosum (De Not.) Martin

Basionym: Sordaria perfidiosum De Notaris in Comm. Soc. Critt. Ital. II, Pt. III, p. 481, 1867. (Reference not seen here). Transferred to Anthostomella by Saccardo, Syll. fung. 1, p. 286, 1882, where the above reference is given.

33. Hypoxylon poliosum (Ell. & Ev.) Martin

Basionym: Rosellinia poliosa Ellis & Everhart in Bull. Torrey bot. Club 22: 439, 1895.

34. Hypoxylon protuberans (Karst.) Martin

Basionym: Rosellinia protuberans Karsten in Bidr. Kann. Finl. Nat. Folk. p. 49, 1873.

35. Hypoxylon quercinum (Hart.) Martin

Basionym: Rosellinia quercina Hartig in Unters. forstbot. Ins. Munch. 1: 1, 1880.

36. Hypoxylon radiciperdum (Massee) Martin

Basionym: Rosellinia radiciperda Massee in Kew Bull. 3, 1896.

- 37. **Hypoxylon rostrosporum** (Gerard) Martin (N.B. neuter epithet ending). Basionym: *Sphaeria rostrospora* (sic.) Gerard in Bull. Torrey bot. Club 5: p. 26, 1874. (Probably changed to 'rostrispora' by Saccardo with nov. comb. *Anthostomella rostrispora* (Ger.) (Sacc.).
- 38. **Hypoxylon sublimbatum** (Dur. & Mont.) Martin Basionym: *Sphaeria sublimbata* Dur. & Mont., Flore d'Algerie, Cryptogamie **1:** 498, 1846.
- 39. Hypoxylon tassianum (C. & De Not.) Martin Basionym: Rossellinia tassiana Cesati & De Notaris in A. Tassi, Sulla Flora della prov. Senese e Maremma Toscana (Guida di Siena Congr. Sc. Ital. X), Siena: p. 3, 1862.
- 40. **Hypoxylon truncatulum** Martin, nom. nov. Basionym: *Rosellinia truncata* Sydow in Philipp. J. Sci. C, **9,** (2): 166, 1914. (Non *Hypoxylon truncatum* (Scw. ex Fr.) Miller.
- Hypoxylon victoriae (Syd.) Martin
 Basionym: Rosellinia victoriae Sydow in Annls mycol. 6: 483, 1908.
- 42. **Kretzschmaria arntzenii** (Theiss.) Martin Basionym: *Penzigia (Sarcoxylon) arntzenii* Theissen in Annls mycol. **6:** 346, 1908.
- 43. **Kretzschmaria atrosphaerica** (Cooke & Massee) Martin Basionym: *Hypoxylon atrosphaericum* Cooke & Massee apud Cooke in Grevillea **22:** 68, 1894.
- 44. Kretzschmaria chardoniana (Miller) Martin Basionym: Penzigia chardoniana Miller apud Chardon & Toro, Mycol Explor. Venezuela, Monogr. Univ. P. Rico phys. biol. Sci. No. 2: 211, 1934.
- 45. **Kretzschmaria deusta** (Hoffm. ex Fr.) Martin Basionym: *Sphaeria deusta* Hoffman ex Fries, Syst. mycol. **2:** 345, 1823.
- Kretzschmaria frustulosa (Berk & Curt.) Martin
 Basionym: Hypoxylon frustulosum Berkeley & Curtis apud Berkeley in
 J. Linn. Soc., Lond. 10: 383, 1868.
- Kretzschmaria pavimentosa (Ces.) Martin Basionym: *Hypoxylon pavimentosum* Cesati in Atti Acc. Sci. fisich. mat. Napoli 8, n. 3: p. 18, 1879.
- 48. **Kretzschmaria rehmii** (Theiss) Martin Basionym: *Stilbohypoxylon rehmii* Theissen in Annls mycol. **6:** 344, 1908.
- Kretzschmaria tuckeri Lloyd apud Stevenson & Cash in Bull. Lloyd Libr.
 (Mycol. Ser. 8): p. 9, 1936. (Not strictly valid, as without Latin diagnosis).

50. Kretzschmaria verrucosa (Miller) Martin

Basionym: Pensigia verrucosa Miller in Bothalia 4: 261, 1942.

51. Kretzschmaria zonata (Lév.) Martin

Basionym: Sphaeria zonata Léveille in Ann. Sci. nat. Ser. 3, Bot, 3: 48, 1845.

52. Lopadostoma apiculatum (Currey) Martin

Basionym: Sphaeria apiculata Currey in Trans. Linn. Soc. 22: 326, 1859.

53. Lopadostoma caespitosum (Ell. & Ev.) Martin

Basionym: Rosellinia caespitosa Ellis & Everhart in Proc. Acad. nat. Sci. Philad.: 327, 1894.

54. Lopadostoma conorum (Fuckel) Martin

Basionym: *Amphisphaeria conorum* Fuckel in Fungi Rhenani (Exsiccata) No. 2653, (?Fasc. 27. ?1874) (Reference not seen.)

55. Lopadostoma cubiculare (Fr.) Martin

Basionym: Sphaeria cubicularis Fries, Syst. mycol. 2: 477, 1823.

56. Lopadostoma decipiens (DC. ex Fr.) Martin

Basionym: *Sphaeria decipiens* DC. ex Fries, Syst. mycol. **2:** 371, 1823. (*Sphaeria decipiens* De Candolle in Lamarck & DC., Flore Francaise, ed. **3,** 2: p. 285, 1805.)

57. Lopadostoma formosum (Ell. & Ev.) Martin

Basionym: Anthostoma formosum Ellis & Everhart in Proc. Acad. nat. Sci. Philad.: 344, 1894.

58. Lopadostoma helveticum (Fuckel) Martin

Basionym: Phaeosperma helvetica Fuckel in Symb. mycol. p. 224, 1869.

59. Lopadostoma microecium (Ell. & Ev.) Martin

Basionym: Anthostoma microecium Ellis & Everhart in Proc. Acad. nat. Sci. Philad.: 344, 1894.

60. Lopadostoma ostropoides (Rehm.) Martin

Basionym: *Anthostoma ostropoides* Rehm in Ber. naturw. Ver. Schwaben No. **26**, 1881. No. 520.

61. Lopadostoma rhenanum (Fuckel) Martin

Basionym: Fuckelia rhenana Fuckel in Fungi Rhenani Exsiccati, Suppl. Fasc. 6, No. 2053. 1867.

62. Lopadostoma sphinctrinum (Fr.) Martin (Not 'sphinctinum')

Basionym: Sphaeria sphinctrina Fries in Kunze & Schmidt, Mykol. Hefte 2: 48, 1823.

63. Numulariola albosticta (Ell. & Morgan) Martin

Basionym: *Nummularia albosticta* J. B. Ellis & Morgan in Bull. Torrey bot. Club **24:** 135, 1897.

- 64. Numulariola australis (Cooke) Martin
 - Basionym: Nummularia australis Cooke in Grevillea 11: 148, 1883.
- Numulariola bacillum (Mont.) Martin (N.B. neuter epithet ending).
 Basionym: Thamnomyces bacillum Montagne in Ann. Sci. Nat. Ser. 2, 8: 358, 1837.
- Numulariola bartholomaei (Peck) Martin
 Basionym: Hypoxylon bartholomaei Peck in Bull. N.Y. State Mus. 150 (1910): 56, 1911.
- 67. Numulariola bilabiata (Speg.) Martin
 Basionym: Camillea bilabiata Spegazzini in Boln Acad. nac. Cienc.
 Cordoba 11: p. 131 of reprint (?p. 511 of original), 1889.
- 68. Numulariola broomeiana (Berk, & Curt.) Martin
 Basionym *Hypoxylon broomeianum* Berkeley & Curtis apud Berk. in
 Grevillea 4: 94, 1876.
- Numulariola cincta (Ferd. & Winge) Martin
 Basionym: Nummularia cincta Ferdinandsen & Winge in Bot. Tidskr.
 29, p. 15.
- Numulariola cinereo-lilacina (Miller) Martin (not 'cineraceo-lilacinum in J. S. Afr. Bot. 35 (5): 292, 1969).
 Basionym: Hypoxylon cinereo-lilacinum Miller in Mycologia 25: 324, 1933.
- Numulariola cyclisca (Mont.) Martin
 Basionym: Hypoxylon cycliscum Montagne in Ann. Sci. Nat. Ser. 4, 3: 122, 1855.
- Numulariola cyclops (Mont.) Martin
 Basionym: Camillea cyclops Montagne in Ann. Sci. nat. Ser. 2, 13: 353, 1840.
- 73. Numulariola cylindrophora (E. & E.) Martin Basionym: *Hypoxylon cylindrophorum* Ellis & Everhart apud C. L. Smith in Bull. Labs Nat. Hist. St. Univ. Iowa 2: p. 407, 1893.
- Numulariola diatrypeoides (Rehm) Martin Basionym: Hypoxylon diatrypeoides Rehm in Annls mycol. 5: 525, 1907.
- Numulariola divergens (Theiss.) Martin
 Basionym: Nummularia divergens Theissen in Annls mycol. 6: 349, 1908.
- Numulariola doidgei (Miller) Martin
 Basionym: Hypoxylon doidgei Miller, A Monograph of the World Species of Hypoxylon: 110, 1961.
- Numulariola flosculosa (Starb.) Martin
 Basionym: Nummularia flosculosa Starback in Bih. K Svenska Vet. Akad.
 Handl. Stockholm 27: Afd. 3, No. 9, p. 11, 1901.

78. Numulariola fossulata (Mont.) Martin

Basionym: Hypoxylon fossulatum Mont. in Ann. Sci, nat. Ser. 4, Bot, 3: p. 123, 1855.

79. Numulariola fuscella (Rehm) Martin

Basionym: Nummularia fuscella Rehm in Annls mycol. 2: 176, 1904.

80. Numulariola glycyrrhiza (B. & C.) Martin

Basionym: *Hypoxylon glycyrrhiza* Berk. & Curt. in J. Acad. nat. Sci. Philad. **2**(2): p. 285, 1853. (Reference not seen.)

- 81. Numulariola grenadensis (Miller) Martin. (N.B. feminine epithet ending.) Basionym: *Hypoxylon grenadense* Miller, A Monograph of the World Species of Hypoxylon: p. 110, 1961.
- 82. Numulariola guaranitica (Speg.) Martin

Basionym: Nummularia guaranitica Spegazzini in Anal. Soc. Cient. Argent. 18: 268, 1884.

83. Numulariola hemisphaerica (Miller) Martin

Basionym: *Hypoxylon hemisphaericum* Miller, A Monograph of the World Species of Hypoxylon: p. 115, 1961.

84. Numulariola heterostoma (Mont.) Martin

Basionym: Sphaeria heterostoma Montagne in Ann. Sci. Nat. Ser. 2, 13: p. 358, 1840.

85. Numulariola hypophlaea (Berk. & Rav.) Martin

Basionym: Diatrype hypophlaea Berkeley & Ravenel in Grevillea 4: 95, 1876.

86. Numulariola hypoxyloides (Karst.) Martin

Basionym: Camarops hypoxyloides Karsten in Bidr. Kann. Finl. Nat. Folk: 53, 187 (Mycologia fennica, 3), 1873.

87. Numulariola labella (Mont.) Martin

Basionym: Camillea labellum Mont. in Ann. Sci. nat. Ser. 4, Bot. 3: p. 113, 1855.

88. Numulariola leprieurii (Mont.) Martin

Basionym: Hypoxylon leprieurii Montagne in Ann. Sci. Nat. Ser. 2, 13: 352, 1840.

89. Numulariola lutea (Alb. & Schw. ex Fr.) Martin

Basionym: *Sphaeria lutea* Albertini & Schweinitz ex Fries, Syst. mycol. 2: p. 347, 1823.

90. Numulariola macromphala (Mont.) Martin

Basionym: Hypoxylon macromphalum Montagne in Ann. Sci. Nat. Ser. 4,3: 122, 185.

91. Numulariola macula (Schw.) Martin

Basionym: Sphaeria macula Schweinitz in Schr. Nat. Ges. Leipzig 1: 31, 1822.

92. Numulariola maculata (Theiss) Martin

Basionym: Nummularia maculata Theissen in Annls mycol. 6: 348, 1908.

93. Numulariola melanaspis (Mont.) Martin

Basionym: Sphaeria melanaspis Montagne in Ann. Sci. Nat. Ser. 2, 13: 357, 1840.

94. Numulariola microspora (Karst.) Martin

Basionym: *Phaeosperma microsporum* Karsten in Mycologia Fennica (*Bidr. Kann. Finl. Nat. Folk*) Pt. 2: p. 53, 1873. Later transferred by Karsten to *Anthostoma microsporum* (Karst.) Karst. in Acta Soc. Fauna Fl. fenn., 2, No. 6: p. 75, 1885.

95. Numulariola nummularia (Bull. ex. Fr.) Martin

Hypoxylon nummularium Bull. ex. Fr.

Champ. Pl. 1: 179, 1791.

Basionym: Sphaeria nummularia (Bull. ex Fr.,) Syst. mycol. 2: 348, 1823.

96. Numulariola mucronata (Mont.) Martin

Basionym: Camillea mucronata Mont. in Ann. Sci. Nat. Ser. 4, 3: p. 112, 1855.

97. **Numulariola petersii** (Berk. & Curt.) Martin (not Lloyd's species which is *Hypoxylon parksii*.)

Basionym: Hypoxylon petersii Berk & Curt. in J. Linn, Soc., Lond. 10: p. 384, 1869.

- 98. Numulariola philippinensis (Ricker) Martin (N.B. Feminine epithet ending). Basionym: *Nummularia philippinensis* Ricker in Philipp. J. Sci. 1, Suppl. 4: p. 280, 1906.
- 99. Numulariola pithodes (B & Br.) Martin

Basionym: Diatrype pithodes Berk. & Broome in J. Linn. Soc., Lond. 14: p. 124, 1873.

100. Numulariola punctulata (Berk. & Rav.) Martin

Basionym: Diatrype punctulata Berk. & Ravenel in Grevillea 4: 94, 1876.

101. Numulariola pyrenocrata (Theiss) Martin

Basionym: Ustulina pyrenocrata Theissen in Annls mycol. 6: 347, 1908.

102. Numulariola rumpens (Cooke)

Basionym: Diatrype rumpens Cooke in J. Linn. Soc., Lond., Bot. 17: 143, 1878.

103. Numulariola scriblita (Mont.) Martin

Basionym: *Hypoxylon scriblita* Montagne in Ann. Sci. Nat. Ser. 4,3: 119, 1855.

104. Numulariola sinuosa (Theiss) Martin

Basionym: Nummularia sinuosa Theissen in Annls mycol. 6: 349, 1908.

105. Numulariola sulcata (Starb.) Martin

Basionym: *Hypoxylon sulcatum* Starbäck in Arkiv Botan. 2, No. 5: p. 20, 1904.

106. Numulariola theissenii (Syd) Martin

Basionym: Nummularia theissenii Sydow in Annls mycol. 7: 344, 1909.

107. Numulariola tubulina (A. & S. ex Fr.) Martin

Basionym: *Sphaeria tubulina* Albertini & Schweinitz ex Fries, Syst. mycol. **2:** 346, 1823.

108. Numulariola venezuelensis (Miller) Martin

Basionym: Nummularia venezuelensis Miller in Chardon & Toro, Mycol. Explor. Venezuela, Monogr. Univ. Puerto Rico, Ser. B, No. 2: 209, 1934.

109. Podosordaria appendiculata (Perd. & Winge) Martin

Basionym: Xylaria appendiculata Ferdinandsen & Winge in Bot. Tidsskr., **29:** p. 17, 1908.

110. Podosordaria aristata (Mont.) Martin

Basionym: Xylaria aristata Montagne in Ann. Sci. Nat., Ser. 4, Bot. 3: 106, 1855.

111. Podosordaria axifera (Mont.) Martin

Basionym: Xylaria axifera Montagne in Ann. Sci. Nat, Ser. 4, Bot, 3: 107, 1855.

112. Podosordaria copelandii (Henn.) Martin

Basionym: Xylaria copelandii Hennings in Hedwigia 47: 260, 1908.

113. Podosordaria filiformis (Alb. & Schw. ex Fr.) Martin

Basionym: Sphaeria filiformis Albertini & Schweinitz ex Fries, Syst. mycol. 2: 329, 1823.

(Sphaeria filiformis Alb. & Schw., 1805—pre-starting date).

114. Podosordaria furcata (Fr.) Martin

Basionym: *Sphaeria dichotomica* Leveille in Ann. Sci. Nat. Ser. 3,3: p. 45, 1845, nec Montagne. *Xylaria furcata*, Nov. Symb. Myc., p. 128, 1851 (? First ref.)

115. Podosordaria heloidea (Penz. & Sacc.) Martin

Basionym: Xylaria heloidea Penzig & Saccardo in Malpighia 11: 498, 1897.

- 116. **Podosordaria hippotrichoides** (Sow.) (not "hippotrichioides") Martin Basionym: Sphaeria hippotrichoides Sowerby, but before 1821. Difficult to establish who first published the name after that date. It appears in Fries, Summa Veg. Scand: p. 382, 1846, as Rhizomorpha.
- 117. Podosordaria kurziana (Currey) Martin Basionym: Xylaria kurziana Currey in Trans. Linn. Soc. Ser. 2, Bot. 1: 129, 1876.
- 118. Podosordaria pyramidata (Berk. & Br.) Martin Basionym: Xylaria pyramidata Berkeley & Broome in J. Linn. Soc., Lond. 14: 118, 1873.
- Podosordaria nigripes (Klotz) Martin
 Basionym: Sphaeria nigripes Klotzsch in Linnaea 7: 203, 1832.
- Podosordaria rhizophila (Cooke & Massee) Martin.
 Basionym: Xylaria rhizophila Cooke & Massee apud Cooke in Grevillea
 22: 37, 1893.
- 121. Podosordaria sicula (Pass. & Belt.) Martin Basionym: Xylaria sicula Passerini & Beltrani in Trans. R.Accad. Lincei, Roma, Ser. 3, 7: 36, 1882.
- 122. Podosordaria thyrsus (Berk.) Martin Basionym: Sphaeria thyrsus Berkeley in Ann. Mag. Nat. Hist. 10 (Suppl.): p. 384, published Jan. 1843.
- 123. Podosordaria truncata (Pat. & Gaill) Martin Basionym: Kretzschmaria truncata Patouillard & Gaillard in Bull. trimest. Soc. mycol. Fr. 4: 109, 1888.
- 124. **Podosordaria ustorum** (Pat.) Martin. (Not "ustora")
 Basionym: Poronia ustorum Patouillard in Bull. trimest. Soc. mycol. Fr. 3: 175, 1887.
- 125. Xylaria cranioides (Sacc. & Paol.) Martin Basionym: Penzigia cranioides Saccardo & Paoletti in Atti Ist. Veneto Sci., 6 Ser., 6: pp. 387–428, 1888 (Mycetes Malacenses No. 100) (Reference not seen).
- 126. Xylaria avellana (Ces.) Martin
 Basionym: Hypoxylon avellana Cesati in Atti Accad. Sci. fis. mat. Napoli
 8 No. 3: 18, 1879.
- Xylaria ayresii (Berk.) Martin
 Basionym: Hypoxylon ayresii Berkeley apud Cooke in Grevillea 11: 132, 1800.

128. Xylaria macrospora (Penz. & Sacc.) Martin

Basionym: Pensigia macrospora Penzig & Saccardo in Malpighia 11: 494, 1897.

129. Xylaria enteroleuca (Speg.) Martin

Basionym: Hypoxylon enteroleucum Spegazzini in Anales Mus. nac. B. Aires 6: 264, 1899.

130. Xvlaria rickii (Theissen) Martin

This was published as *Xylaria rickii* by Theissen in Annls mycol. **6:** p. 342, 1908, and transferred to *Xylobotryum* (as "*Xylobrotrium*") by Lloyd, C. G., in Mycological Writings **7:** p. 1350, 1925.

The following combinations have been published elsewhere, at an earlier date:

Kretschmaria turbinata (E & E) Lloyd, Mycological Writings 6, (Mycological Notes, 65, p. 1033, 1921).

Hypoxylon aquilum (Fr.) Brefeld, Untersuchungen aus dem Gesammtgebiete der Mykologie, Heft 9: 259, 1891.

Hypoxylon subaenum (Berk. & Curt.) Speg.

Basionym: *Sphaeria subaenea* Berk. & Curt. in J. Linn. Soc., Lond. **10** (46): p. 387, 1868. Transfer to *Hypoxylon subaenum* already made by Spegazzini in Anal. Soc. Cient. Argent. **26**: p. 32 (p. 30 of reprint), 1888.

Lopadostoma juglandinum (Rehm) Saccardo & Trotter, Syll. Fung. 22, 374, 1913.

The following combination must be rejected for lack of sufficient information:

Hypoxylon subacutum (Schw.) Martin. The basionym is untraceable. The specimen in the NVBG, Fink 1149, Mayaguez, Puerto Rico, (1915) is labelled as **Rosellinia subacuta** (Schw.) Sacc., whereas possibly *R. subiculata* was intended. It is certainly close to that species (now merged with *Hypoxylon chrysoconium*) but lacks a subiculum.

Holotypes and Latin descriptions of new species:

York, 1925.

Anthostomella cavarica (Petrak) Martin. Initial publication not yet traced, but the material in the NYBG is clearly labelled as the type. Stromata minutissima, in ligno immersa, substrata discolorata, cum uno aut paucis peritheciis; ascosporae aequae, pallide brunneae, $5.5 \times 20.0\mu$. Holotypus: Weisskirchen, in ligno *Ligustrum* vulgaris, New

Anthostomella inconspicua Martin, nom. nov.

Stromata minuta, uniperitheciata, 400–600 μ ; ostiolata papillata; ascosporae ellipticae, pallide brunneae, 3.0–3.5 x 9.0–11.0 μ .

Synonym: Sphaeria picacea Cooke & Ellis in Grevillea 7, p. 9, 1878. Holotype: Ellis, N. Amer. Fungi 183 (date?), in the Herbarium, New York Botanical Garden. Also the type of Anthostoma picaceum (C & E) E & E in N. Amer. Pyren. 578, 1892. Anthostomella picacea (C & E) Saccardo in Syll. Fungi I, 293, 1882, is also based on Sphaeria picacea, but the holotype material in the NYBG is a separate collection from the above: Ellis 2846. Vaccinium, Newfield, NJ, (1878).

Hypoxylon adumbratio Martin. Holotype: Martin 288. Hypoxylon aridicolum Martin. Holotype: Martin 508. Hypoxylon aureostroma Martin. Holotype: Martin 268.

Hypoxylon conicum Martin

Stromata uniperitheciata, conica aut ovala, 900–1 400 x 1 100–2 000 μ ; ostiola inconspicua, papilata; ascosporae ellipticae, fusco-brunneae, 5.0–7.5 x 21.0–30.5 μ . Holotypus: *Baker 188* in Fungi Malayana, Mt Maquiling, Philippines, (1914) (NYBG).

Synonym: Rosellinia horrida Rehm in Leafl. Philipp. Bot. 8: p. 2941 1916. non Rosellinia horrida Hazlinsky, 1873 (See Saccardo's Syll. fung. 1: p. 273.)

Hypoxylon cuneosporum Martin. Holotype: Martin 302. Hypoxylon daldiniforme Martin. Holotype: Martin 546. Hypoxylon entololeucum Martin. Holotype: Martin 362. Hypoxylon ludovicianum Martin. Holotype: Martin 1718.

Hypoxylon minutissimum Martin. *Martin 269*. Hypoxylon occidentale Ellis & Morgan ex Martin.

Stromata pulvinata aut aplanata, purpura, verrucosa, $2.5-53 \times 2.5-135 \times 0,5-2,0$ mm; peritheciae $400-600 \times 500-900 \mu$; ascosporae fuscobrunneae, $4.5-6.5 \times 8.0-12.5 \mu$.Ab *Hypoxylon rubiginosum* differtur stromatibus differentiatibus. Holotypus: *Morgan 621* in lignis *Liriodendron*, Ohio, USA.

Hypoxylon pulchrum Martin

Stromata uniperitheciata, hemisphaerica, $800-1\,500~\mu$, nigra, cum ostiolis prominentis conicis; in subiculo brunneo. Asci cylindrici, $110-120~x~7-8~\mu$, ascosporae fusoidae, appendiculatae, 5.0-7.5~x~16.5-

18.5 μ . Holotypus: *Parker* in Herb. Young Nat. Soc. 160, in ligno *Abies*, Seattle, (1892) (NYBG).

Synonym: Rosellinia pulcherrima Ellis & Everhart in Erythea 1: 197, 1893. (Hypoxylon pulcherrimum is already occupied by Hohnel in Annls mycol. 3: 187, 1905.)

Hypoxylon plumbinum Martin. Holotypus: Martin 376.

Hypoxylon sphaeriosporum Martin. Holotypus: Martin 555.

Hypoxylon viridicolor Martin. Holotypus: Martin 487.

Lopadostoma stictoides (E & E) Martin.

Stromata in ligno immersae, ostiolis albis; ascosporae fuscobrunneae, $11.0 \times 17.5 \mu$. Ab *Lopadostoma ostropoides* differtur ascosporis *parvulis*. Holotypus: *Dearness* in herbario Ellis & Everhart *1899*, in ligno *Crataegus*, London, Ontario, (1892) (NYBG).

Numulariola linearis Martin.

Stromata elliptica, parva, intus luridus: ascosporae aequae, ellipticae vel cylindricae, fuscobrunneae, 3.5 x 8.0 μ .Ab *Numulariola morgani* differtur ascosporis parvulis. Holotypus: *Martin 1155*, in ligno Lake Ozark, Missouri.

Numulariola morgani Miller ex Martin.

Stromata aplanata, effusa, intus luridus; ascosporae aequae, ellipticae, fuscobrunneae, 7.0 x 17.0 μ . Holotypus: *Morgan 362*, in ligno *Juglans cinerea*, Preston, Ohio (1897) (Miller Herbarium).

Numulariola signata Morgan ex Martin.

Stromata parva, orbiculata, intus magnus; ascosporae aequae, fuscobrunneae, $4.5 \times 10.5 \mu$. Holotypus: *Shear*, in ligno *Gleditsia triacanthos*, Sterlington, Louisiana, (1934) (Miller Herbarium).

Podosordaria plumosa Martin. Holotypus: Martin 410.

A CASE OF MYOPHILY INVOLVING DROSOPHILIDAE (DIPTERA)

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ABSTRACT

The relationship between the xerophytic stapeliad Caralluma schweinfurthii (Stapelieae, Asclepiadaceae) and certain species of Drosophilidae (Diptera) has been studied under seminatural conditions. Data on the plant, the insect visitors and the adaptation involved in terms of pollination ecology are given. Seven species of Drosophila and two species of Zaprionus are deceptively attracted to the flowers which chemically mimic the natural breeding substrate. This appears to be the first reported instance of myophily involving Drosophilidae. Evolutionary aspects are briefly discussed and the need for field observations emphasized.

UITTREKSEL

'N GEVAL VAN MIOFILIE WAT DROSOPHILIDAE (DIPTERA) RAAK

'n Studie, onder semi-natuurlike toestande, is gemaak van die verhouding tussen die zerofitiese plant Caralluma schweinfurthii (Stapelieae, Asclepiadaceae) en sekere spesies van die Drosophilidae (Diptera). Gegewens oor die plant, die insekbesoekers en die aanpassing ten opsigte van bestuiwingsekologie word aangebied. Sewe spesies van Drosophila en twee van Zaprionus word op 'n misleidende wyse tot die blomme aangelok deur na-apery van die voedingsmedium. Hierdie blyk die eerste aangemelde geval van miofilie te wees wat Drosophilidae impliseer. Ewolusionêre aspekte word kortliks bespreek en die behoefte aan verdere veldstudies beklemtoon.

Introduction

Stapeliads (tribe Stapelieae, family Asclepiadaceae) are a characteristic feature of the African flora, with many hundreds of species in over a score of genera known (White and Sloane, 1937). A few species are known from adjacent areas, but the majority are concentrated in Africa with the arid parts of southern Africa being very rich in species: sixteen of the twenty genera described by White and Sloane have representatives there. There is extensive variation between flowers of the various species as regards colour, patterning, size, type and distribution of hairs, surface sculpture of corolla and other features. This strongly suggests adaptation to specific pollinators as Proctor and Yeo (1973: 300 et seq.) have pointed out. Little is known, however, concerning the pollination ecology of stapeliads, apart from the observation that some of the larger species, for example Stapelia gigantea N. E. Brown and Stapelia nobilis N. E. Brown, attract carrion flies by means of their deceptive floral odour. The deception in this case is so effective that oviposition around the central disk of the flower

often occurs. As the stapeliads have pollinaria (i.e. pollinia with associated structures) rather like those of Orchidaceae, there is thus an interesting opportunity for research into the determination of their pollinators and the relationships between the two.

In the case described here, a hitherto unreported group of pollinators, namely Drosophilid flies, is shown to be active in pollination and thus the spectrum of stapeliad myophily (adaptation to pollination by flies) is broadened. The attraction based on odours simulating decomposing organic matter, or the natural breeding substrate, has led to the further distinction of sapromyophily, so that this term could just as well be applicable in the present case.

MATERIAL AND METHODS

1. The myophilous plant

The case described involves the small, leafless xerophyte *Caralluma schwein-furthii* Berger. It has recently been shown (Leach and Plowes, 1966) that this species includes *Caralluma piaranthoides* Obermeijer.

The plant is a small, jointed, procumbent perennial consisting of soft, fleshy stems growing up to 5 or 6 cm above the soil in which it is shallowly rooted. The species is widely distributed in central and south-central Africa. The known distribution, taxonomic citations and details of flower structure are given by Leach and Plowes (1966) while a colour photograph of the flower has been published by Plowes (1971:10). Observations were made on a cultivated plant of unknown origin, grown outdoors in Johannesburg during the period 19 February to 4 April, 1973 when the plant was in flower. The months of February and March are the regular flowering period of the plant in Johannesburg and these months, when the weather is warm and humid, correspond with the peak time of drosophilid activity in the area.

The plant was observed intermittently over the period mentioned previously for a total of ca 6 hours during daylight.

2. The insect visitors

Visitors were aspirated individually from the flowers and preserved in alcohol for cataloguing and later identification. For a few days, while the plant was kept indoors, a trap of rotting pineapple (Ananas comosus L.) seeded with yeast suspension was set up outdoors to sample the local insect population attracted to such bait. Specimens were netted, preserved, catalogued and identified as before. A few drosophilids bearing pollinia were prepared for scanning electron microscopy by dehydration and subsequent coating with gold; these were viewed and photographed in a Cambridge 'Steroscan' instrument.



Fig. 1.
Flower of *C. schweinfurthii*.
Scale = 5 mm

RESULTS

1. Visitors

Drosophilids were avidly attracted to the flowers for a few hours after sunrise and before sunset. At these cooler times of the day the flies were very active on the flowers which emitted a strong odour variously described as "over-ripe fruit with hint of orange" and "sour beer". It may be noted that it is well-known that a particular flower can evoke seemingly different olfactory responses in different persons, as judged by their responses. During the heat of the day, flies were not active and odour could not be detected. No insects other than Drosophilidae were observed to be attracted to the flowers. There was no differential attraction between the sexes of the visitors, and both males and

females appeared to be equally capable of acting as carriers of pollinia. Even while the plant was kept indoors for a few days, a few flies still managed to find their way to the plant, showing that even over some distance the flowers effectively advertise their presence.

A careful search for deposited eggs was made on the flowers and none was found, so it may be concluded that oviposition does not take place on the flowers; possibly, the appropriate tactile responses needed for this are absent. It may be noted that oviposition always occurs on fruit-traps.

The results of sampling drosophilids visiting both flowers and fruit-trap are given in Table 1.

 ${\it Table~1.}$ ${\it DATA~ON~VISITORS:}$ NUMBERS OF DROSOPHILIDAE, BY SPECIES, CAUGHT ON FLOWERS OF ${\it CARALLUM~SCHWEINFURTHII}$ AND TRAPPED WITH FRUIT BAIT

	with (+) pollinia	flowers	traps	total	χ ^{2**}
Drosophila busckii Coquillett	_	0	6	6	7,85
Drosophila immigrans Sturtevant	+	62	40	102	0,74
Drosophila melanogaster Meigen (males)	+	2	2	4	
Drosophila sp. (repleta group)*	_	2	1	3 }	0,37
Drosophila punctatonervosa Frey	_	2	0	2]	
Drosophila simulans Sturtevant (males)	+	21	10	31	1,57
$Drosophila\ melanogaster + simulans\ (females)$	+	13	10	23	0,00
Zaprionus tuberculatus Malloch	_	6	10	16	2,37
Zaprionus vittiger Coquillett	+	8	10	18	1,08
		116	89	205	13,98***

^{*} Possibly an undescribed species—specimens catalogued under WWR 20G.

The results of trapping on the flowers and in the fruit-trap were compared by means of a χ^2 -test of homogeneity. The test shows a significant difference between flowers and trap regarding the capabilities for attracting the different species. However, it is clear that one species, D. busckii, contributes more than half the total χ^2 -value and this species is known to breed in proteinaceous substrates. The presence of D. busckii at the fruit-trap is doubtless due to opportunistic feeding, while the other species represent true fruit-breeding species and behave in accordance with the hypothesis that the flowers are as

^{**} X₂ computed by apportioning the total catch for each species, weighted according to the column totals to give expected numbers in each cell, on the assumption of no differential attractivity.

^{***} d.f. = 6; 0.05 > P > 0.01.

attractive to them as the fruit. The χ^2 -values for the remaining species are each non-significant. It may be concluded that the flowers, by simulating the odour(s) of the natural breeding substrate, mimic the latter and effectively deceive the drosophilids into visiting the plant when in flower.

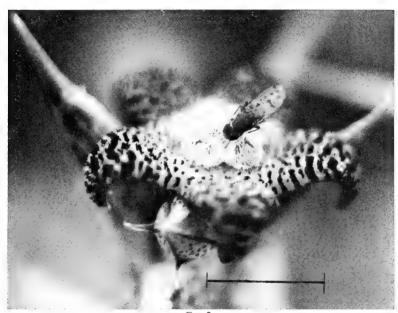


FIG. 2.

Drosophila punctatonervosa visiting flower; note unopened bud.

Scale = 5 mm

2. Results on pollination

The flower (Fig. 1) is small, in colours of yellow and maroon. Excepting a few older stems, each one of about 40 stems carried a few clusters of buds (2–6 buds per cluster) in various stages of development although only a few flowers were open simultaneously. According to Leppik's (1968) morphogenetic classification, the flower belongs to his class 4: pleomorphic, showing radial symmetry and at the pluriform evolutionary level, but a specialised form deviating from the general trend.

In the bud stage, the five corolla lobes are connate at the tips, as may be seen in Fig. 2. As soon as the first lobe started peeling back, flies would enter the chamber formed by the remaining lobes, so that by the time the flower was fully

opened all the pollinia had been removed. One flower, specifically watched, had all five pairs of pollinia present at 0600 and all removed at 0645 hours. Removal of pollinia is thus rapid. Attachment of the pollinaria (pollinia plus associated structures) to the proboscis of the fly takes place while the fly is tapping with the proboscis on the corona (Fig. 2). Eight individuals, belonging to several species (Table 1) were recovered with attached pollinia; in one case (Fig. 3), two pairs of pollinia were attached to a single fly. None of the captured specimens with pollinia had them attached anywhere but on the proboscis, where the corpusculum and retinacula (or translator arms) were affixed to the shaft of the proboscis. The attachment appears to be a firm one as individuals with pollinia. kept alive overnight in glass vials, did not lose them. Little inconvenience appeared to be caused to the insect, and behaviour appeared normal, as suggested by the observation that one fly (Zaprionus vittiger) had managed to pick up two pairs. On one occasion, a fly with pollinia on a front leg was observed on a stem of the plant: the front legs were being rubbed together as if in an effort to dislodge the attached masses. How they got there in the first place is not known.

Actual pollination, that is release of the pollinia onto a recipient flower, was unfortunately not observed. It is possible, even likely, that there must be a time delay between picking up the pollinia and their release in order to minimize the likelihood of self-pollination. This delay could operate by means of a mechanism involving maturation of part of the associated structures which attach the pollinia to the vector. It is not known whether the plant is self-sterile or not as no artificial pollinations were done. At any rate, even under the best of conditions, the rate of effective delivery of pollinia must be very low, as in the case with orchids where the mechanism is similar. As the pollen is delivered *en masse*, van der Pijl and Dodson (1966) have described this as a "dangerous gambling-mechanism of a long-term strategist". However, in this precision gambling there is ultimate efficiency because if the pollinia are actually delivered, only one visit is required to fertilize hundreds or thousands of ovules.

In the present case, release of pollinia would most likely take place near the corona which is the appropriate place for growth of the pollen tubes to effect fertilization; here the structure of the corona is such that the pollinia would be engaged by the anther wings for detachment. As collecting disturbed the whole aggregation of flies each time, many of the carriers probably did not return to the flowers. Certainly only a small fraction of the very many pollinia removed were recovered by capture of flies bearing them.

DISCUSSION

Two important points arising from the preceding sections and the evolutionary significance of the adaptation require discussion.

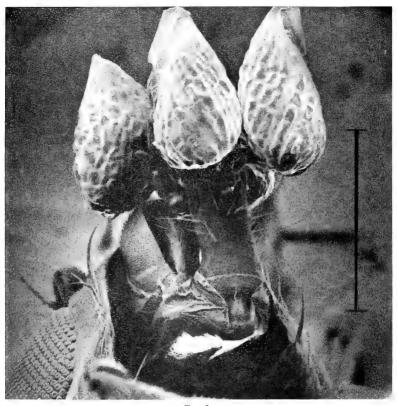


Fig. 3. Ventral view of head of Zaprionus vittiger showing two pairs of attached pollinia. Scale = 0.5 mm

1. Is the case a genuine one of myophily?

According to Faegri and van der Pijl (1966), myophilous flowers are adapted for pollination by flies, and exhibit a complex of characteristics associated with this adaptation; the complex describes a syndrome. Twelve features which may contribute to a complex have been given by these authors (op. cit.), although not all may be present in any specific case. The syndrome of myophily is well-developed in certain genera of the Asclepiadaceae and Orchidaceae (Faegri and van der Pijl, 1966; van der Pijl and Dodson, 1966); in the latter family, four

large groups in the most divergent genera have become myophilous, indicating that the adaptation has repeatedly arisen independently.

In the case described here, features positive (+) for these are tabulated below:

	eral syndrome of myophily n Faegri & van der Pijl, 1966)	Present case (C. schweinfurthii flowers)
A.	Anthesis at different times	+
B.	No zygomorphy; radial flat or trap-like	+
C.	Large landing surface with osmophores	+
D.	Colour dull or greenish, occasionally augmented by brown-purple with checkered or dotted designs	+
E.	Odour putrescent	+
F.	Nectar or other food usually absent	+
G.	No nectar guides	+(*)
H.	Perianth often with slits or holes in side	
I.	Perianth often with transparent window-guides	_
J.	Brown furry hair cover	_
K.	Vibratile hairs ("Flimmerkorper" or oscillators)	_
L.	Trap devices guiding visitors or catching or holding them	+

^{*} A flower preserved in alcohol was viewed under UV light (wavelength 254 nm) and no guides were visible.

Characters H-L inclusive tend to be shown in flowers that physically trap the visitors, which does not happen in this case. Thus the evidence from: (a) chemical mimicry of the feeding (and for the drosophilids sampled, also breeding) substrate; (b) positive attraction of potential pollinators; (c) capture of five different species carrying pollinia; (d) features of the flower indicative of myophily; and (e) correspondence between flowering time and peak dorsophilid activity allows of the conclusion that C. schweinfurthii is, indeed, specifically adapted for pollination by Drosophilidae.

2. Which species of Drosophilidae are the actual pollinators in the field?

The observations reported here do not necessarily establish that any or all of the visitors are the actual pollinator(s) where the plant grows naturally. The objection that the plant was studied out of its natural area of occurrence loses most of its validity when it is borne in mind that the species listed in Table 1 (with the possible exception of *D. punctatonervosa*) are widespread over all of central and southern Africa. Two points must be borne in mind here: firstly, experience with other entomophilous flowers indicates that it is unlikely that the plant is monophilic or strictly tied to a single pollinator, although such cases do occur. Rather, it would appear that it may well be oligophilic or adapted

to a group of similar (in size) or closely related species which, as an evolutionary strategy, would be safer for long-term survival. The fact that several drosophilid species of more or less similar size can pick up the pollinia would support this view. Secondly, some of the species listed in Table 1, for example *D. immigrans*, *melanogaster* and *simulans*, are colonizing species and are now virtually cosmopolitan; their geographic origin is uncertain (Dobzhansky, 1965). The *Zaprionus* species, however, are restricted to Africa (ten or more species) and south-east Asia (a few species) and may well be effective pollinators in the wild. The species *Z. tuberculatus* and *Z. vittiger* are widespread in Africa. Information as to the actual pollinator(s) can come only from field studies, but it is clear that whatever species are actually involved the plant is adapted to small, fruit-breeding drosophilids.

3. Evolutionary aspects

Van der Pijl and Dodson (1966) have drawn attention to the fact that sapromyophilous flowers are most numerous in warm arid zones especially in Africa but that, curiously, this switch to Diptera is not paralleled in similar zones in the Americas; they suggest that the switch to Diptera in Africa is a long-standing one related to the dominance of flies there. It would thus be of great interest to have comparative information on the pollination ecology of the numerous stapeliads occurring in Africa as this would, doubtless, show an evolutionary connection between their radiation and that of Diptera.

It is very likely that there are no fewer than 2 000 extant species of Drosophilidae (Hardy, 1965; Wheeler and Hamilton, 1972) with about half of the known species in the large genus Drosophila Fallén; these have been the subject of a large number of investigations conducted in both the laboratory and field. As is to be expected, there is a wide diversity of ecological niches exploited for both feeding by the adults and for nutritional support of the larvae during development. Breeding sites are typically fallen fruit, fleshy fungi, flowers (both fresh and fallen) or other plant material in the initial stages of decay where associated yeasts and bacteria are consumed by the drosophilids. While feeding by adults is opportunistic the breeding sites tend to be more carefully selected with the behaviour of the ovipositing females accordingly adapted and some species are exceedingly specialised in this regard. To date, the reverse situation, namely where a particular plant species is specifically adapted for pollination by drosophilids has not been described. Such a case, described here, is therefore of double interest, both to students of evolution in stapeliads and drosophilids.

It is known (Free, 1970) that drosophilids may be effective in the pollination of certain field crops, for example guayale (the composite *Parthenium argentatum*

A. Gray), and some of the flower-breeding drosophilid species may be incidentally involved in pollination, but none of these cases shows specific adaptation entirely on the part of the flower, which is the essential feature of myophily.

Of particular interest in the present case is the observation that while Drosophilidae are deceived into investigating the flowers, wastage of eggs does not occur (as it does with the larger carrion flies) and thus the deception is not counterselective to responsive insects. This suggests that the adaptation is a long-standing one, more ancient than the one between the larger stapeliads and carrion-flies.

CONCLUSIONS

- 1. The flowers of *Caralluma schweinfurthii* are adapted for pollination by drosophilids ("fruit-flies").
- 2. The insect visitors are attracted by chemical mimicry of the natural breeding and/or feeding substrate, i.e. the relationship is one of sapromyophily.
- 3. Nine species of Drosophilidae in two genera were observed to visit the flowers, and four of the species were observed to act as pollen-vectors.
- 4. The need for field observations over the range of the plant's distribution is emphasized in order to confirm or modify the above findings.
- The case described is the first reported one of myophily where Drosophilidae are involved.

ACKNOWLEDGEMENTS

I thank the following persons: Mrs Enid du Plessis (CSIR, Pretoria) for improvements in the paper; Mrs L. Davidson, (Curator of the Moss Herbarium, University of the Witwatersrand) for bibliographical assistance; Mr. J. J. Lavranos (Johannesburg) for information on stapeliads; Professor N. van Schaik (Department of Genetics, University of the Witwatersrand) for helpful suggestions; Dr R. A. Dyer (National Botanical Garden, Pretoria) for confirming my identification of the stapeliad; Dr Leonidas Tsacas (Paris, France) for confirming and, in some cases, correcting my identifications of Drosophilidae; Mr L. P. Fatti (Department of Applied Mathematics, University of the Witwatersrand, Johannesburg) for help with analysis of data; Professor Francisco J. Ayala for reading the paper and making helpful suggestions. Dr P. R. O. Bally (Nairobi, Kenya) for information on the plant.

This was written while on sabbatical leave as Research Fellow in the Department of Genetics, University of California (Davis), and I thank Professor Th. Dobzhansky and Professor F. J. Ayala for extending to me the hospitality of their laboratory.

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EMBRYOLOGY OF JUBAEOPSIS CAFFRA BECC.: 1 MICROSPORAN-GIUM. MICROSPOROGENESIS AND MICROGAMETOGENESIS

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ABSTRACT

Development of the anther wall is of the Basic type. Microsporogenesis is simultaneous and results in the formation of tetrahedral tetrads. Pollen grains, which have a smooth exine.

are monocolpate and at the time of anther dehiscence, the grain is bi-nucleate.

During microgametogenesis, both the vegetative and the generative nuclei migrate into the pollen tube where mitosis of the latter nucleus results in the formation of two male gametes. The vegetative nucleus degenerates progressively from the initial stages of germination of the pollen grain and finally disappears just prior to the formation of the male gametes, J. caffra is apparently a polyploid species.

UITTREKSEL

EMBRIOLOGIE VAN JUBAEOPSIS CAFFRA BECC.: 1. MIKROSPORANGIUM. MIKROSPOROGENESE EN MIKROGAMETOGENESE

Ontwikkeling van die helmknopwand is van die Basiese tipe. Mikrosporogenese is gelyktydig en lei tot die vorming van tetraëdriese tetrades. Stuifmeelkorrels, wat 'n gladde eksien besit, is monokolpaat en is met oopspringing van die helmknop, tweekernig.

Tydens mikrogametogenese beweeg beide die vegetatiewe en die generatiewe kerne in die stuifmeelbuis in waar mitose van die laasgenoemde kern lei tot die ontstaan van twee manlike gamete. Die vegetatiewe kern degenereer progressief vanaf die begin stadia van ontkieming van die stuifmeelkorrel totdat dit net voor die vorming van die manlike gamete heeltemal verdwyn. J. caffra is waarskynlik 'n poliploïede spesies.

INTRODUCTION

Jubaeopsis caffra Becc. is the only palm species which is endemic to the Republic of South Africa and it is confined to two extremely small localities in Pondoland on the east coast, viz. the estuaries of the Mtentu and Msikaba rivers (Robertson & Visagie, 1975).

Considering the scarcity of suitable plant material and the problems involved in obtaining it, it is not surprising that no data relating to the embryology of this species have been recorded. It is strange though that so little is known about the embryology of the Palmae as a whole, especially when the size of this family is taken into account.

The structure of the mature anther wall is remarkably well-known for palms in general (Davis, 1966) but no information on the development of the wall is available. Usually the wall consists of a persistent epidermis, an endothecium with fibrous thickenings, two to six ephemeral middle layers and a glandular tapetum (Davis, 1966). The tapetum cells are uni-nucleate in *Cocos nucifera* (Juliano & Quisumbing, 1931), *Borassus flabellifer* L. (Venkato Rao, 1955a) and *Hyphaene indica* (Mahabale & Chennaveeraiah, 1957) while in *Areca* (Venkato Rao, 1955a) *Pritchardia* (Venkato Rao, 1955b) *Licuala, Livistona* (Venkato Rao, 1956a), *Sabal* (Venkato Rao, 1956b) and *Arecastrum romanzoffianum* (Venkato Rao, 1958) they are bi- or multinucleate.

With regard to microsporogenesis, simultaneous division of the microspore mother cells occur in the majority of genera and species studied viz. Chamaedorea, Areca triandra, Caryota, Pteriogospermum (Schnarf, 1931, cited by Mahabale & Chennaveeraiah, 1957), Cocos nucifera (Juliano & Quisumbing, 1931), Borassus, Areca (Venkato Rao, 1955a) Licuala, Livistona (Venkato Rao, 1956a), Trachycarpus, Sabal (Venkato Rao, 1956b), Hyphaene indica (Mahabale & Chennaveeraiah, 1957), Caryota, Chrysalidocarpus and Arecastrum romanzoffianum (Venkato Rao, 1958). Successive cytokinesis is apparently restricted to Nypa fruticans and Pinanga disticha (Davis, 1966).

The palm pollen grain is binucleate (Brewbaker, 1967) and the mitotic division of the generative nucleus takes place in the pollen tube after the grain has germinated (Read, 1963, 1964). The destiny of the vegetative nucleus is uncertain. Eames (1961) states that the tube nucleus, as it is often called, behaves in different ways and may or may not enter the pollen tube. The activities of this nucleus during microgametogenesis of the palm has not yet been described.

MATERIAL AND METHODS

The material for the study of microsporogenesis and the structure of the anther wall was collected during 1973/74 from inflorescences at various stages of development from a 43 year old tree in St. George's Park, Port Elizabeth. Male flowers were fixed in Craf II (Sass, 1958), dehydrated in an ethyl alcohol/tertiary butyl alcohol (TBA) series, embedded in paraffin wax (55°C) and sectioned at 10 μ m on a rotary microtome as prescribed by Brooks, Bradley and Anderson (1950). The sections were stained in safranin/fast green (Holtzhausen, 1972).

Prior to studying microgametogenesis, it was necessary to germinate pollen grains of *J. caffra*. Although various methods were used for this, the most successful method proved to be the coated-slide technique (Conger, 1953 cited by Sharma & Sharma, 1972). Optimum results were obtained with ten per cent sucrose and 0,01 per cent boric acid in agar. To ensure that a large number of metaphase figures would be obtained, 0,05 per cent colchicine was added to the medium. Pollen from flowers which had been collected a day earlier was sprinkled onto the coated slides and incubated in the light at 25°C in a plastic container which had been lined with moist filter paper. By fixing and staining at various times, it was established that the most metaphase figures were ob-

tained after 18-20 hours of incubation.

After incubation, the slides were fixed in acetic acid/alcohol (1:3) for 12 hours. Thereafter, dehydration by means of a TBA series and staining with propiono-carmine (Vasil, 1963) took place. The stained slides were made permanent by means of the alcohol vapour method (Brooks *et al.*, 1950).

The scanning electron microscopic study was conducted on a Jeol JSM-U3 microscope with fresh pollen, which had been coated with palladium gold (Robbertse, 1974).

RESULTS AND DISCUSSION

Each anther is composed of four microsporangia (Fig. 1). This condition is maintained throughout the lifetime of the anther and is still evident at the time of dehiscence of the anther and, although the wall separating the two sporangia in each lobe becomes crushed, it does not break down completely (Fig. 1).

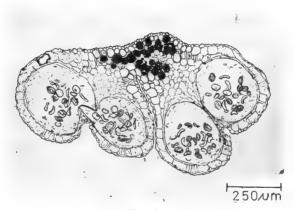
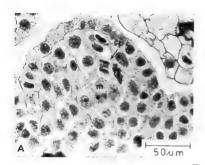


Fig. 1. A transverse section through the anther of J. caffra.

Initially the anther comprises the connective plus four lobes of undifferentiated homogeneous cells. As soon as the tip of the inner bract enveloping the inflorescence becomes visible in the axil of the leaf, periclinal divisions occur in the hypodermal cells of the anther. This division results in the formation of two cell layers *viz*. an outer one which constitutes the primary parietal layer and an inner cell layer, the primary sporogenous layer.

The latter layer undergoes mitotic divisions in both anticlinal and periclinal directions. Thereafter the cells enlarge and their nucleoli become conspicuous (Fig. 2A). These cells constitute the microspore mother cells.

The cells of the primary parietal layer divide periclinally to produce the two secondary parietal layers. The cells of these two layers in turn enlarge and divide periclinally as well (Fig. 2A) to produce four cell layers between the epidermis of the anther or microsporangium and the sporogenous tissue (Fig. 2B). Of these four layers the outermost one will differentiate to form the endothecium; the innermost cell layer *i.e.* adjacent to the sporogenous cells, develops into the tapetum and the two remaining layers constitute the middle layers of the anther wall.



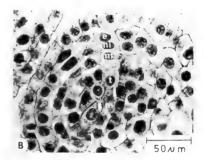


Fig. 2.

Transverse sections of the lobe of a young anther.

Periclinal divisions of the two secondary parietal layers (spc.).

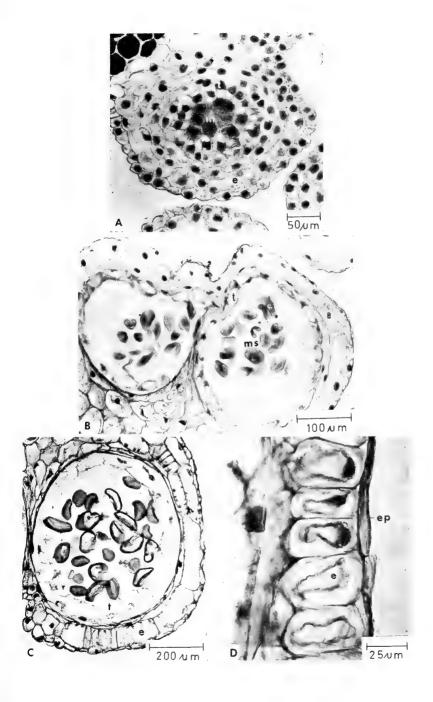
B. The four cell layers constituting the anther wall viz, endothecium (e), two middle layers (ml) and the tapetum (t).
 Also visible in both figures are the microspore mother cells (m).

In the anther wall of *J. caffra*, two middle layers occur and each of the two secondary parietal layers are involved in their formation. It is concluded thus that the Basic type (Davis, 1966) of anther wall formation is found in this species. According to Davis this type of development represents a primitive condition. Some difference of opinion concerning the various components of the anther wall, especially in respect of the tapetum, is to be found in the literature. According to Eames (1961), the primary sporogenous cells divide periclinally to give rise to both the tapetal cells and the sporogenous cells. This is in direct contrast to the reports by Maheshwari (1950) and Davis (1966) both of whom state that the tapetum has a non-sporogenous origin and that it is derived solely from the

Fig. 3.

A-C Transverse sections of microsporangia showing the development of the various cell layers at different stages of development.

Longitudinal section through the wall of a mature anther. (e-endothecium; ep-epidermis; m-microspore mother cells; ms-microspores; t-tapetum).



parietal tissue. The above data show clearly that in *J. caffra* the tapetum is derived from the parietal tissue only.

During the early stages of the ontogeny of the anther, the epidermis cells of the anther wall are more or less isodiametric in shape in a transverse section through the anther (Fig. 2A). During subsequent growth, the surface area of the anther increases very rapidly and although anticlinal divisions do occur in the epidermis cells, they cannot keep pace with the increase in volume of the underlying cells. Consequently the epidermis cells become stretched and flattened in a tangential plane (Fig. 3B & C) but the cells are not cast off. The epidermis is therefore of a persistent nature.

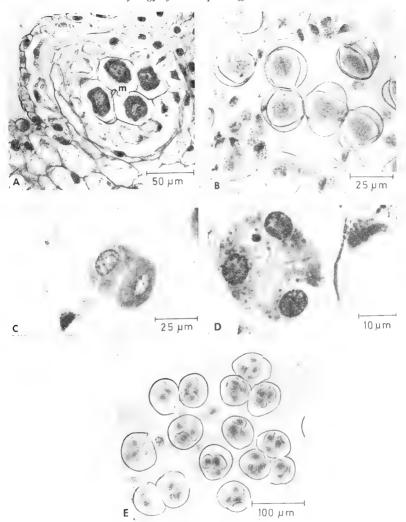
The endothecium cells steadily increase in the size until the completion of meiosis (Fig. 3B). At maturity the characteristic "fibrous" thickenings are present as bars across the radial cell walls (Fig. 3C). These bars are visible only in a transverse section through the anther and not in a longitudinal section (Fig. 3D).

Development of the "fibrous" thickenings is not initiated until the microspore tetrads separate into individual pollen grains (Fig. 3B & C). Although the thickenings occur mainly in the endothecium cells, they can also be observed in the cells of the outer middle layer, especially in the vicinity of the connective (Fig. 3C). This phenomenon has been reported in a number of other monocotyledons e.g. Agave, Crinum and the Zingiberaceae (Davis, 1966). A large number of starch grains are present in the older endothecium cells.

The cells of the two middle layers do not undergo anticlinal divisions and soon become tangentially stretched and radially flattened (Fig. 3B). These two cell layers are ephemeral and become crushed and degenerate sometime prior to the onset of meiosis in the microspore mother cells (Fig. 4A). The outer layer is however relatively more persistent than the inner middle layer.

The tapetum cells remain uninucleate. They form a single layer around the sporogenous tissue and become radially elongated and are initially closely packed against each other with no intercellular spaces between them (Fig. 3A). This condition is short lived though, and as the two middle layers degenerate and the circumference of the sporangium increases the tapetum cells become loosely arranged, but maintain a more or less radial orientation. After meiosis, the radial organisation is no longer evident and the cells of the tapetum remain only as a thin layer around the periphery of the anther loculus (Figs. 3B & C).

At this stage *i.e.* after the formation of the pollen grains, the walls of the tapetum cells are still intact and remain *in situ* and consequently it is concluded that the tapetum of *J. caffra* is of the glandular or secretory type (Maheshwari, 1950). This is in accordance with the condition found in other palms (Davis, 1966) and is the type of tapetum most commonly found in the dicotyledons and advanced or more specialised monocotyledons (Eames, 1961).



- Fig. 4.

 Microsporogenesis in J. caffra.

 A. Microspore mother cells (m) shortly prior to meiosis.

 B. Prophase I.

 C. Telophase I. Note the absence of a dividing wall.

 D. Telophase II showing the first signs of cell wall formation.

 E. A squash preparation of the tetrahedral microspore tetrads.

Microsporogenesis

The primary sporogenous cells do not function directly as the microspore mother cells but first undergo a limited number of mitotic divisions. These mother cells are very different from the surrounding tissues in that they are large cells with dense cytoplasm, large nuclei and prominent nucleoli (Fig. 4A).

Initially the cell walls between the mother cells are thin (Fig. 4A) but shortly before meiosis, the cell walls become very much thicker (Fig. 4B).

As in most other palms (Davis, 1966) cytokinesis is of the simultaneous type (Maheshwari, 1950) and no cell wall is formed after the first division (Fig. 4C). Wall formation is delayed until after Telophase 2 (Fig. 4D). The actual division results from cell-plate formation.

The microspore tetrads are tetrahedral (Fig. 4E). At the completion of meiosis the tetrad is surrounded by a thick callose wall. This wall however degenerates soon afterwards and the microspores are released into the anther loculi.

Each microspore is initially enclosed in a thin wall which becomes thicker shortly prior to dehiscence of the anther. The exine is relatively thin and smooth without any spines. The pollen grain is monocolpate (Fig. 5) and elongate with a furrow or fold on the distal side. This is in accordance with other palms



Fig. 5. Stereoscan micrograph of the pollen of *J. caffra*.

(Parthasarathy, 1970). According to Eames (1961) this type of pollen grain is a primitive feature characteristic of the monocotyledons. The fully imbibed pollen grain is 40 μ m in diameter.

Male gametophyte and gametogenesis

Shortly prior to dehiscence of the anther, the large centrally placed nucleus of the microspore divides mitotically and the vegetative and generative nuclei are formed. The vegetative nucleus remains more or less round and centrally situated while the generative nucleus, which is spindle shaped, is confined to the periphery of the microspore (Fig. 6A). The pollen grain is released from the anther in this condition, *i.e.* 2-celled. These findings are in accordance with those of Brewbaker (1967) and Read (1963, 1964) for other palm species.

Germination of the pollen grain is initiated one hour after sowing and by this time the vegetative nucleus has degenerated extensively and is only just visible (Fig. 6B).

In *J. caffra* the vegetative nucleus occasionally disappears completely before the generative cell has entered the tube. In most cases though, the tube nucleus does not disappear completely and faint traces of it remain visible until the late stages of mitosis of the generative nucleus (Figs. 6C & D).

It seems unlikely that a nucleus in such a state of degeneration and disorganisation could play any active role in the growth of the tube. It is consequently suggested that the movement of this nucleus into the pollen tube is purely a passive action and that the tube nucleus is simply borne along by the cytoplasmic flow from the pollen grain into the pollen tube.

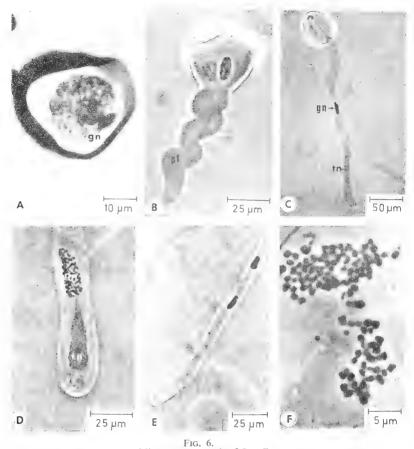
The spindle-shaped generative cell moves down into the tube soon after germination of the grain, but its nucleus does not undergo mitosis until at least 20 hours after sowing. Division of the generative cell results in the formation of the two male gametes (Fig. 6E). At this stage the pollen tube is between 600 and 900 μ m long.

Chromosome counts

The pollen tube and its haploid nucleus provides material which is well suited for the studying of the chromosome complement of a given plant species. This method has been used with great success by Read (1963, 1964, 1965, 1966; Read & Moore, 1967) specifically on palm material.

According to Read (1966) the subfamily Cocoideae can be divided into two groups on the basis of chromosome complement. The spiny bactroid group e.g. *Bactris* and *Acrocomia* with n=15 is the first while the second group has n=16. The latter group includes *Jubaea chilensis* and *Cocos nucifera*.

It appears from the results of this study that *J. caffra* is a polyploid (Fig. 6F). Owing to the large number and small size of the chromosomes, it was not pos-



Microgametogenesis of J. caffra.

- Mature pollen grain with vegetative and spindle-shaped generative nuclei. Germination one hour after sowing. Both nuclei are still visible.
- C. Five hours after sowing. Note the remains of the tube nucleus.

 D. Metaphase during mitosis of generative nucleus.

- Two male gametes in pollen tube 20 hours after sowing. The vegetative nucleus is no longer visible.
- Squash preparation of the pollen tube and generative nucleus during metaphase of
 - (gn-generative nucleus; pt-pollen tube; tn-tube nucleus; vn-vegetative nucleus).

sible to make a precise count of the chromosome number. However, as shown in Fig. 6F, the haploid complement is in the order of 100 chromosomes. Only one other polyploid palm has been reported, viz. Arenga, a dwarf caryotoid palm from Malava (Moore & Uhl, 1973) with n=32.

CONCLUSION

From the results of this study, it would seem that J. caffra exhibits a number of primitive features. Development of the anther wall, for example, is of the Basic type, which according to Davis (1966) is the most primitive type. Unfortunately no information concerning this aspect is available for any other palm.

The pollen of this palm species, like that of the majority of palms, is monocolpate. Pollen of this type is considered by Sowunmi (1967, cited by Moore & Uhl, 1973) as being the most primitive pollen found in the monocotyledons.

While Moore & Uhl (1973) state that the basic haploid chromosome complement of palms is 18, Read (1966) reports that the majority of Cocoid palms have a haploid complement of 16 chromosomes. This suggests that the Cocoid palms in general are more specialised than the primitive Coryphoid and Phoenicoid palms which have n=18 chromosomes. J. caffra however has a haploid complement of between 80 and 100 chromosomes and is almost certainly a polyploid. In this respect it is unique in that only one other polyploid palm, viz. Arenga, is known which has n=32.

ACKNOWLEDGEMENTS

The University of Port Elizabeth and the C.S.I.R. made research facilities and financial grants available for this study.

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'N HERSIENING VAN DIE *AGATHOSMA*-SPESIES VAN KOMMER-SIËLE BELANG

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UITTREKSEL

Duidelike verskille ten opsigte van die morfologie en chemiese samestelling van die blare van die kommersieel belangrike Agathosma-soorte het daartoe gelei dat A. crenulata (L.) Pillans onderverdeel word in A. crenulata (L.) Pillans pro parte en A. serratifolia (Curt.) Spreeth comb. nov. 'n Derde spesie, A. betulina (Berg.) Pillans, word behou soos dit deur Pillans (1950) in sy hersiening van die genus erken is.

In hul natuurlike habitats is geen plante met 'n blaarvorm, wat 'n tussenvorm tussen enige twee van die bogenoemde soorte sou kon verteenwoordig, gevind nie. 'n Verspreidingskaart vir die drie spesies, tabelle en illustrasies, sowel as 'n sleutel om tussen hulle te onderskei,

word gegee.

ABSTRACT

A REVISION OF THE COMMERCIALLY IMPORTANT AGATHOSMA SPECIES

Marked differences in leaf morphology and chemical composition of the commercially important Agathosma species have led to the subdivision of A. crenulata (L.) Pillans into A. crenulata (L.) Pillans pro parte and A. serratifolia (Curt.) Spreeth comb. nov. A third species, A. betulina (Berg.) Pillans is retained in accordance with the revision of the genus by Pillans (1950). No specimens with an intermediate leaf-form between any two of the abovementioned species have been found in their natural habitats.

A distribution map of the species, tables and illustrations, as well as a key for distinguish-

ing between the species, are given.

INLEIDING

. Die Agathosma-spesies wat kommersieel van waarde is vir die verkryging van boegoe-olie is endemies in die Suidwes-Kaap en kom veral voor in die distrikte Clanwilliam, Citrusdal, Piketberg, Tulbagh, Stellenbosch en Swellendam tussen oosterlengtegrade 18° tot 22° en suidebreedtegrade 31° tot 35°.

Net drie soorte is van kommersiële belang, naamlik rondeblaarboegoe (bergboegoe), ovaalblaarboegoe en langblaarboegoe (kloofboegoe). Laasgenoemde word die laaste aantal jare nie meer bemark nie.

Voordat die twee genera *Barosma* en *Agathosma* deur Pillans in 1950 verenig is, het die kommersieel belangrike boegoesoorte onder die genus *Barosma* geressorteer. Drie soorte is erken, naamlik *B. betulina* (Berg.) Bartl. & Wendl. (bergboegoe of rondeblaarboegoe), *B. crenulata* (L.) Hook. (ovaalblaarboegoe) en *B. serratifolia* (Curt.) Willd. (langblaarboegoe of kloofboegoe).

^{*&#}x27;n Verkorte deel van 'n skripsie wat ingelewer is ter gedeeltelike vervulling van die vereistes vir die graad Magister Scientiae aan die Universiteit van Stellenbosch. Vir publikasie aanvaar 3 Oktober 1975.

Pillans erken net twee boegoe-spesies onder die genus Agathosma, naamlik A. betulina en A. crenulata. Ten spyte van die groot verskil in blaarvorm, asook die verskil in geografiese verspreiding tussen die vroeëre B. crenulata en B. serratifolia het hy hierdie twee spesies verenig onder die naam Agathosma crenulata (L.) Pillans. Kommersieel word ook onderskei tussen die bevolkings wat Pillans bymekaar gevoeg het, nl. die sogenaamde ovaalblaarboegoe wat bemark word en langblaarboegoe wat glad nie in aanvraag is nie.

In sy sleutel gebruik Pillans kenmerke van die blare en vrugbeginsels om tussen sy twee spesies te onderskei: die blare van A. betulina is breër in die boonste helfte (omgekeerd eiervormig), terwyl dié van A. crenulata breër is in die onderste helfte. In die huidige ondersoek kon hierdie verskil nie bevestig word nie (Fig. 2). 'n Verdere verskil, volgens Pillans, is dat die vrugbeginsel van A. betulina omgekeerd eiervormig-bolvormige prosesse dra, terwyl dié prosesse by A. crenulata eiervormig-bolvormig is. Laasgenoemde kenmerke kon, in die huidige ondersoek, nie by die twee soorte waargeneem word nie.

Uit gesprekke met taksonome in die vernaamste Suid-Afrikaanse herbaria, het dit geblyk dat dit dikwels moeilik is om herbariumeksemplare op grond van hierdie verskille uit te ken. Omdat daar dus onsekerheid bestaan in verband met die uitkenning van die genoemde taksa, het 'n hersiening van die kommersieel belangrike *Agathosma*-soorte noodsaaklik geword.

1. Morfologiese ondersoek

'n Volledige anatomiese studie van die blare, stingels en wortels van die boegoesoorte het getoon dat die anatomie van hierdie organe soveel ooreenstem dat dit nie gebruik kan word om die soorte van mekaar te onderskei nie.

Die spesies is ook vergelyk ten opsigte van die blomme en vrugte. Klein verskille in die graad van behaardheid by die blomdele, die vorm en kleur van die kroonblare en die vorm van die staminodia wat wel waargeneem is, is nie konstant nie en is dus taksonomies van geen waarde nie.

Die blomme van die betrokke spesies stem ooreen in die volgende: Die blomme is enkeld, okselstandig op die boonste gedeelte van jong takke, of in okselstandige gevurkte byskerms met drie of meer blomme of op 'n kort okselstandige takkie met twee tot ses blomme. Wanneer daar net een blom in die oksel van 'n blaar is, is die blomsteel 0,6–7 mm lank met twee teenoorstaande, groen, gesteelde steelblaartjies redelik hoog aan die steel asook 'n aantal kleurlose, sittende hoogteblaartjies (soms tot 9) by die basis van die blombodem. In geval van 'n byskerm beskik die oudste blom gewoonlik oor vier* gesteelde groen steelblaartjies, terwyl jonger blomme net twee het en in die oksel van 'n skutblaar gedra word.

^{*}Volgens Lanjouw (1968) word selde 4 steelblaartjies by Dicotyledoneae aangetref.

Die vyf kelkblare is blywend, vry, groen, 2,5–4,0 mm lank, eiervormig of lansetvormig, die proksimale helfte membraanagtig verbreed, die rande gaaf met enkele hare daarop. Die vyf kroonblare is vry, 7–10 mm lank, lansetvormig, wigvormig by die basis, met hare op die rande asook adaksiaal by die basis en met enkele hare hoër op op die hoofaar; subterminaal effens geswolle met baie oliekliere adaksiaal naby die hoofaar; gewoonlik wit of ligpers van kleur. Die skyf is ringvormig, intrastamineaal, gewoonlik met vyf vlesige lobbe teenoor die helmdrade.

Die tien meeldrade kom in twee kranse van vyf voor met die buitenste krans antepetale meeldrade gewysig tot staminodia. Die staminodia is wit, 3–5,5 mm lank, ingeplant op die rand van die skyf tussen die skyflobbe, abaksiaal stomp gekiel, langwerpig-lansetvormig met hare op die rande vir byna die hele lengte sowel as adaksiaal, maar abaksiaal slegs by die basis; die rande effens ingerol naby die punt wat eindig in 'n klieragtige knoppie. Die helmdrade is op die rand van die skyf teenoor die vlesige skyflobbe ingeplant, behaard vir byna die hele lengte. Die helmknoppe is regopstaande met die helmdrade aan die basis daarvan aangeheg sodat die helmknoppe beweeglik is, onbehaard of verspreid ylbehaard.

Die bostandige vrugbeginsel bestaan uit vyf byna vrye vrugblare en is vertikaal gelob met kort gesteelde kliere daarop, elke lob met een horisontaal geplaasde, lepelvormige harige uitsteeksel aan die distale punt; dit is vyfhokkig met 2 epitrope saadknoppe in elke hok, waarvan een steriel is. Die styl is ongeveer 6 mm lank met die onderste gedeelte harig en tussen die vruglobbe ingeplant en die stempel is enkelvoudig en effens na een kant teruggebuig.

Die doosvrug is hokspletig. Die endokarp raak by rypheid los van die mesokarp en bly meestal vasgeklem om die saad. Die sade is ellipsoïed, effens afgeplat, redelik hardskalig en glansend swart van kleur.

Skandeerelektronmikroskopiese foto's van die stuifmeelkorrels het getoon dat ook hier geen noemenswaardige verskille tussen die soorte is nie.

Aangesien feitlik die enigste morfologiese verskille tussen die boegoesoorte by die blare gevind is, is die spesies ten opsigte hiervan deeglik vergelyk en uit Tabel 1 en 2, waarin die spesies t.o.v. blaarmorfologie vergelyk word, blyk dit dat daar wel drie boegoesoorte onderskei word, soos die ouer taksonome gedoen het.

Die resultate wat in Tabel 1 weergegee word, is as volg verkry: van elke lokaliteit waar herbariummateriaal versamel is, is vyf blare per plant gemeet en die gemiddeldes is vir die verskillende soorte uitgewerk. Vir die lengte/breedte verhouding van die laminas (Tabel 2) is die standaardfout bereken volgens die metode van Snedecor (1959).

Die verspreiding van die oliekliere in die blare van die drie boegoesoorte het geen noemenswaardige diagnostiese verskille getoon nie.

TABEL 1 'n Tabel om die blare van die drie boegoesoorte morfologies te vergelyk.

	A. betulina (rondeblaar)	A. crenulata (ovaalblaar)	A. serratifolia (langblaar)
Lengte van die petiolus in mm	1	2	1,5
Gemiddelde lengte van die lamina in mm	20,4	22,9	34,9
Gemiddelde breedte van die	20,1	22,5	5-1,5
lamina in mm	12,9	10,9	6,5
Vorm van lamina	breed ellipties tot byna rond	langwerpig- ellipties	smal-ellipties
Punt van die lamina	afgerond en teruggebuig	afgerond	byna spits
Basis van die lamina	wigvormig	wigvormig	wigvormig

'n Tabel om die verhouding van die lengte tot die breedte van die laminas van die drie boegoesoorte te vergelyk.

Soort	Aantal bepalings	Verhouding Lengte/Breedte		
A. betulina	60	1,95±0,06		
A. crenulata	35	$2,34\pm0,07$		
A. serratifolia	25	$5,35\pm0,27$		

In hulle natuurlike habitats is geen plante met 'n blaarvorm, wat 'n tussenvorm tussen enige twee van die soorte sou kon verteenwoordig, gevind nie.

2. BIOCHEMIESE ONDERSOEK

(a) Aminosure, suikers en organiese sure in die blare.

In die Afdeling Plantfisiologie van die Departement Plantkunde, Universiteit van Stellenbosch, is 'n ondersoek gedoen om die drie boegoesoorte te vergelyk ten opsigte van die aminosure, suikers en organiese sure in die blare.

Wat die aminosure en suikers betref, is geen noemenswaardige verskille aangetref nie. Geen betekenisvolle verskille is by suksiensuur en sitroensuur aangeteken nie.

Die appelsuurinhoud van die blare is semi-kwantitatief bepaal en die bevindings word in Tabel 3 weergegee. Hierdie resultate is 'n gemiddelde van drie monsters wat elk drie keer gechromatografeer is.

Uit hierdie bepalinge van die appelsuurinhoud van die blare, blyk dit duidelik dat die verskillende bevolkings wat ondersoek is as aparte spesies beskou kan word. Daar is weliswaar 'n groter verskil tussen die twee taksa wat deur Pillans (1950) saamgevoeg is as tussen A. betulina (Berg.) Pillans en A. serratifolia (Curt.) Spreeth. Die appelsuurinhoud van blare van A. crenulata (L.) Pillans (sonder A. serratifolia) onderskei hom baie duidelik van die ander twee.

(b) Chemiese samestelling van die olie.

In die Departement Chemie, Universiteit van Stellenbosch, is die olie wat van die blare van die drie verskillende boegoesoorte verkry is, gaschromatografies ondersoek.

Wat die samestelling van die olie betref, is A. betulina duidelik onderskeibaar van die ander twee op grond van die pulegoon-, 4-diosfenol- en diosfenolinhoud van die olie, maar daar is geen noemenswaardige verskille tussen die olies van die ander twee soorte gevind nie.

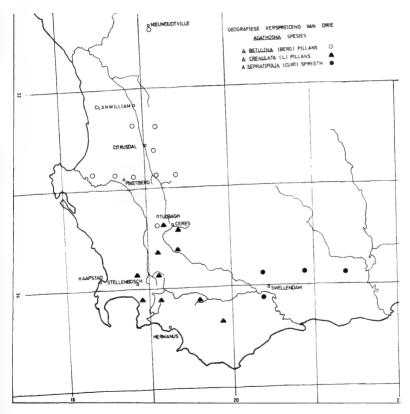


Fig. 1. Geografiese verspreiding van drie Agathosma-species.

3. GEOGRAFIESE VERSPREIDING

Die materiaal in die vernaamste Suid-Afrikaanse herbaria is nagegaan en die gegewens wat so verkry is, sowel as die gegewens verkry uit persoonlike waarnemings van vars materiaal is gebruik. 'n Kaart (Fig. 1) wat die vindplekke van elke spesie aandui, is volgens die ruitverwysingsmetode, soos aanbeveel deur die Navorsingsinstituut vir Plantkunde, Pretoria, opgestel.

A. betulina (bergboegoe of rondblaarboegoe).

Soos die volksnaam, bergboegoe, aandui, groei die spesie in bergagtige dele en gewoonlik in arm, sanderige grond. Dit word vanaf Ceres noordwaarts aangetref tot in die Pakhuisberg naby Clanwilliam en is al versamel in die volgende distrikte: Ceres, Tulbagh, Piketberg, Citrusdal, Clanwilliam en Calvinia. Die verspreidingsgebied van hierdie spesie oorvleuel met dié van *A. crenulata* in die Winterhoekberge naby Tulbagh. Dit word volop aangetref in die Sederberge waar dit uiters droë toestande in die somer oorleef. Volgens Von Wielligh (1913) groei hierdie soort teen berghange tussen 334 m en 668 m bo seespieël en dit floreer in rooi sanderige grond met rooi sandsteen.

A. crenulata (ovaalblaarboegoe).

Die verspreidingsgebied strek vanaf Tulbagh suidwaarts tot by Bettysbaai. Na die weste word dit tot by Stellenbosch, die Paarl en Wellington aangetref en die oostelike grens van die verspreidingsgebied loop deur Ceres, Wolseley, Worcester en Caledon. Dit groei gewoonlik in koel, beskutte bergklowe naby stroompies, maar oor die algemeen word dit in 'n swaarder grondtipe aangetref as A. betulina. In Jonkershoek en Bainskloof kom dit laag af in die klowe naby lopende water voor, maar dit groei ook hoër op in die berge. By Kluitjieskraal naby Wolseley is dit in sanderige grond ver van enige lopende water aangetref.

A. serratifolia (langblaarboegoe of kloofboegoe).

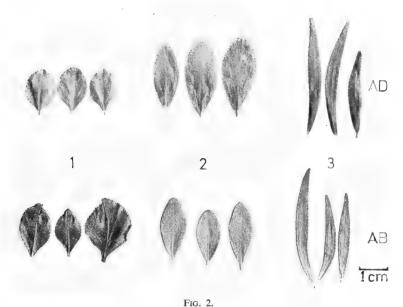
Hierdie spesie word net in die berge in die omgewing van Swellendam en Riversdal aangetref, in beskutte plekke naby vloeiende water. Dit kom dikwels tussen digte struikgewas voor en dan is die grootste gedeelte van die takke sonder blare. Dit groei goed in swart sanderige leemgrond en word meestal aangetref in klam grond in klowe, soms in die skaduwee van bome. Von Wielligh (1913) het dit aangetref tussen 167 m en 334 m bo seespieël. In 'n tuin in Swellendam is daar 'n aangeplante heining van langblaarboegoe (A. serratifolia). Dit groei hier besonder goed in 'n redelike swaar leemgrond.

4. TAKSONOMIE

Daar was in die verlede skynbaar geen onsekerheid oor die omgrensing van A. betulina nie, maar in die huidige ondersoek het dit duidelik geword dat die onderskeidingskenmerke tussen die soorte A. betulina en A. crenulata soos deur Pillans gebruik, ontbreek. Dit is verder opvallend dat hy geeneen van die nomen-

klatoriese tipes van die kommersiële boegoe-spesies te sien gehad het of iets daarvan vermeld nie.

Pillans (1950) verskaf geen rede waarom hy dit nodig geag het om die twee spesies *Barosma crenulata* en *B. serratifolia* saam te voeg onder *A. crenulata* nie. Hy maak ook nie melding van die feit dat daar op grond van die blaarvorm moontlik twee bevolkings bestaan nie, alhoewel hy materiaal uit die areale van beide hanteer het. Die huidige ondersoek toon dat, volgens die verhouding van die lengte tot die breedte van die blare (Tabel 2), die spesie *A. serratifolia* duidelik onderskei kan word, terwyl die ander twee nie so baie verskil nie.



'n Foto van die blare van die drie boegoesoorte om die verskil in blaarvorm aan te toon.

1, Agathosma betulina; 2, A. crenulata; 3, A. serratifolia; AD, adaksiaal; AB, abaksiaal.

'N SLEUTEL OM DIE DRIE SPESIES TE ONDERSKEI

Lamina breed-ellipties tot byna rond of langwerpig-ellipties.

Sinonimie, diagnostiese kenmerke en vindplekke

(a) A. betulina (Berg.) Pillans in Jl S. Afr. Bot. 16: 75 (1950). Tipe: e Cap b. sp. Grubb. s.n. (SBT; holo; STE; foto!).

Hartogia betulina Berg., Descr. Pl. Cap.: 67 (1767), basionym.

Diosma betulina L., Mant. Alt.: 343 (1771); Thunb., Prodr. 43 (1794); ejusd. Diss. Diosm.: 13 (1797); Willd., Sp. Pl. 1: 1140 (1798); Pers., Syn. Pl. 1: 247 (1805); Lodd. Bot. Cab. 5: 404 (1820), non L.; Thunb., Fl. Cap.: 227 (1823); DC. Prodr. 1: 714 (1824); Spreng., Syst. Veg. 1: 785 (1825).

Bucco betulina Roem. & Schult., Syst. Veg. 5: 443 (1819).

Barosma betulina Bartl. & Wendl. in Beitr. Bot.: 102 (1824); Sond. in Harv. & Sond. Fl. Cap. 1: 393 (1860); Engl. in Engl. & Prantl, Pflanzenfam. 3 (4): 149 (1894) & 2te aufl. 19a: 267 (1931); Sim, For. Pl. Cape Col.: 155 (1907); Marloth, Fl. S. Afr. 2: 68 (1925).

Diagnostiese kenmerke: Klein veelstammige struike, hoogstens 1 m hoog met dun geel, rooibruin tot donkerbruin onbehaarde takkies, stam ondergronds vertak sodat dit polvormig vertoon. Blare 14–25 mm \times 6–14 mm, breed ellipties tot byna rond, gemiddelde lengte/breedte verhouding van die lamina 1,95 \pm 0,06; afgerond en effens teruggebuig by die punt; lamina onbehaard met 'n prominente hoofaar en dikwels opvallende sekondêre are abaksiaal met verspreide oliekliere aan die abaksiale kant sigbaar. Bloeistele ongeveer 7 mm lank, onbehaard of met ylverspreide kort hare, okselstandig. Wanneer net een blom in die oksel van 'n blaar voorkom, is die blomsteel ongeveer 7 mm lank. Appelsuurinhoud van die blare, 7,6 mg/g vars materiaal. 4-diosfenol en diosfenol sterk verteenwoordig in die olie, maar pulegoon feitlik afwesig.

VINDPLEKKE (Fig. 1)

KAAPLAND—3119 (Calvinia): Nieuwoudtville (-AC), Leipoldt s.n. (BOL). — 3218 (Clanwilliam): Elandskloof (-BD), Hafström & Acocks 785 (PRE); Schimmelberg (-BD), Pillans 9088 (BOL); 19 km N.W. van Piketberg (-CD), Spreeth 121 (STE); Kapteinskloof, Piketberg (-DC), Pillans 7880 (BOL); Versveldspas, Piketberg (-DD), Esterhuyzen 5511 (BOL).

— 3219 (Wupperthal): Middelberg, Sederberge (-AC), Schlecter 886 (BOL); Uitkykpas (-AC), Gillet 4100 (PRE); Algeria (-AC), Taylor 2944 (PRE); Sederbergpas naby Algeria (-AC), Spreeth 104 (STE); Buffelhoekpas (-CA), Marsh 768 (PRE); Elandskloof, Clanwilliam (-CA), Esterhuyzen 3138 (BOL); Warmbad, langs Olifantsrivier (-CA), Stephens 7116 (BOL); Koue-bokkeveldberge, Citrusdal (-CC), Leighton 1260 (PRE); 32 km S.S.O. van Citrusdal (-CD), Spreeth 113 (STE); Kleinplaas, S.O. van Citrusdal (-CD), Spreeth 114 (STE).

- 3319 (Worcester): 10 km N.N.O. van Tulbagh (-AC), Spreeth 108 (STE).

(b) A. crenulata (L.) Pillans in Jl S. Afr. Bot. 16: 73 (1950) pro parte.

Diosma crenulata L., Cent. Pl. 2: 11 (1756) basionym; ejusd. Amoen. 4: 308 (1759).

D. crenata L., Syst. Nat. ed. 10: 11 (1758); ejusd. Syst. Nat. 3: 182 (1770); Thunb., Prodr.: 43 (1794); ejusd. Diss. Diosm.: 14 (1797); Murr., Syst. Veg.: 250 (1797); Willd., Sp. Pl. 1: 1138 (1798); Pers., Syn. Pl. 1: 247 (1805); Thunb., Fl. Cap.: 227 (1823); Pappe, Fl. Cap. Med. Prodr.: 5 (1850).

D. latifolia Andr., Bot. Rep. t.33 (1797); Lodd., Bot. Cab. 3, t.290 (1818); Spreng. Syst. Veg. 1: 785 (1825).

D. odorata DC., Prodr. 1: 714 (1824).

Parapetalifera odorata Wendl., Coll. Pl. 1: 50 (1805).

Bucco crenata Roem. & Schult., Syst. Veg. 5: 444 (1819).

Baryosma odorata Roem. & Schult., Syst. Veg. 5: 448 (1819).

Barosma crenata Sweet, Hort. Brit. ed. 1: 89 (1826).

B. crenulata Hook. in Curt. Bot. Mag.: 3413 (1835); Sond. in Harv. & Sond. Fl. Cap. 1: 393 (1860); Edmonds & Marloth, Elem. Bot. S. Afr.: 142 (1897); Engl. in Engl. & Prantl, Pflanzenfam. 3 (4): 149 (1897) & 2te Aufl. 19a: 267 (1931); Henslow, S. Afr. Fl. Pl.: 116 (1903); Sim, For. Fl. Cape Col.: 155 (1907); Stoneman, Plants and their ways in S. Afr. ed. 2: 138, 324 (1915); Marloth, Fl. S. Afr. 2: 104 (1925).

Agathosma latifolia Loud., Hort. Brit.: 25 (1830).

Lektotipe: 'n Eksemplaar van Burman is deur Linnaeus in sy Cent. Pl. 2: 11 (1756) benaam as *Diosma crenulata*. Daar is egter nie so 'n eksemplaar in Linnaeus se herbarium in Londen nie, maar wel een (die linkerkantse eksemplaar op vel 270.34) wat in Linnaeus se handskrif *D. crenata* benaam is (persoonlike mededeling deur T. T. Barnard en J. P. Rourke). Aangesien hy *D. crenata* as 'n veranderde spelling van die vroeëre *D. crenulata* beskou het, moet die linkerkantse eksemplaar op vel 270.34 as lektotipe vir die naam *D. crenulata* gebruik word.

Diagnostiese kenmerke: Struike tot 5 m hoog met onbehaarde of gedeeltelik ylbehaarde takke, jong stingels liggroen, maar ouer stingels donkerbruin van kleur. Blare 15–30 mm \times 7,5–13 mm, langwerpig-ellipties, punt afgerond, gemiddelde lengte/breedte verhouding van die lamina 2,34 \pm 0,07; lamina met ten minste die hoofaar prominent aan die onderkant, onbehaard of met enkele hare adaksiaal naby die are, met klein verspreide oliekliertjies sigbaar aan beide kante, maar veral abaksiaal, punt van die lamina afgerond. Bloeistele 15 mm lank, onbehaard of verspreid ylbehaard, okselstandig. Wanneer blomme alleenstaande in die oksel van 'n blaar voorkom, is die blomsteel 8–15 mm lank. Appelsuurinhoud

van die blare 1,2 mg/g vars materiaal. Olie met diosfenol in klein konsentrasie en 4-diosfenol prakties afwesig, maar pulegoon in groot konsentrasie verteenwoordig.

VINDPLEKKE (Fig. 1)

KAAPSTAD—3318 (Kaapstad): Bokant Tweede Waterval in Jonkershoek (-DD), *Thompson 612* (PRE); Swartboskloof (-DD), *van der Merwe 811* (PRE); naby brug oor Eersterivier, Jonkershoek (-DD), *Spreeth 105* (STE).

—3319 (Worcester): 10 km N.N.O. van Tulbagh (-AC), Spreeth 112 (STE); kloof wes van Ceres (-AD), Hutchinson 572 (BOL); Kluitjieskraalbosboustasie naby Wolseley (-CA), Spreeth 107 (STE); naby Bainskloof bosboustasie (-CA), Spreeth 106 (STE); Paradise Ravine, Bainskloof (-CA), Adamson 4395 (PRE); Wellington (-CA), Marloth 486 (PRE); in vallei noord van Limietberg (-CA), Esterhuysen 1638 (BOL); Wagenboomsrivier, Worcester (-CB), Esterhuyzen 8957 (BOL); Turfkloof, Wemmershoekberge (-CC), Wasserfall 558 (NBG).

— 3418 (Simonstad): Lourensford, Hottentotshollandberge (-BB), Esterhuyzen s.n. (BOL); Lourensriviervallei (-BB), Parker 3893 (NBG).

— 3419 (Caledon): Dwarsberg (-AA), Stokoe 8505 (PRE); Genadendal (-BA), Roser 15419 (PRE); Hangklip (-BD), Middlemost s.n. (NBG); Harold Porter Natuurreservaat (-BD), Ebersohn, in NBG 39/68 (NBG); Platbos, Kogelberg (-BD), Boucher 284 (PRE).

(c) A. serratifolia (Curt.) Spreeth, comb. nov.

Diosma serratifolia Curt., Bot. Mag.: 456 (1799) basionym—Ikonotipe.

Baryosma serratifolia Roem. & Schult., Syst. Veg. 5: 448 (1819).

Adenandra serratifolia Link, Enum. Hort. Berol. 1: 239 (1821).

Parapetalifera serrata Wendl., Coll. Pl. 1: 92 (1805).

Barosma serratifolium Engl. in Engl. & Prantl, Pflanzenfam. 3 (4): 149 (1897) & 2te Aufl. 19a: 267 (1931).

Agathosma crenulata (L.) Pillans in Jl S. Afr. Bot. 16: 73 (1950) pro parte.

Diagnostiese kenmerke: Struike tot 3 m hoog met onbehaarde of gedeeltelik ylbehaarde takke, jong stingels donkerbruin van kleur. Blare 17–42 mm \times 4–8 mm, smal-ellipties, gemiddelde lengte/breedte verhouding van die lamina 5,35 \pm 0,27; lamina met meestal 3 are prominent abaksiaal; onbehaard of met enkele haar adaksiaal naby die are; oliekliere veral sigbaar abaksiaal; punt van die lamina byna spits. Bloeistel 10 mm lank, onbehaard of verspreid ylbehaard, okselstandig. Wanneer blomme alleenstaande in die oksel van 'n blaar voorkom, is die blomsteel 6–15 mm lank. Appelsuurinhoud van die blare, 5,4 mg/g vars materiaal. Olie met diosfenol in 'n klein konsentrasie en 4-diosfenol prakties afwesig, maar pulegoon in 'n groot konsentrasie.

VINDPLEKKE (Fig. 1)

KAAPLAND—3320 (Montagu): Doktersbos, 5 km N.O. van Swellendam (-CD), Spreeth 124 (STE); Lemoenshoek, Swellendam (-DD), Esterhuyzen 10490 (BOL).

- 3321 (Ladismith): Langeberg, Riversdal (-CD), Muir 462 (BOL).
- 3420 (Bredasdorp): Swellendam (-AB), Spreeth 123 (STE).

TABEL 3 Appelsuurinhoud van die blare van drie boegoesoorte (mg per g vars materiaal)

A. betulina	A. crenulata	A. serratifolia
7,6	1,2	5,4

BEDANKINGS

Die skrywer wil graag sy opregte dank en waardering aan die volgende persone en instansies betuig:

Dr. J. J. A. van der Walt en prof. M. P. de Vos vir raad en leiding tydens die ondersoek.

Mnr. J. E. Watts en dr. E. E. Bartel vir hulp met die biochemiese ondersoek. Die W.N.N.R. vir finansiële steun en die kurators van die herbaria STE, PRE en BOL en ander persone wat behulpsaam was met die verkryging van materiaal.

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CHEMOTAXONOMIC ASPECTS OF THE BUCHU SPECIES AGATHOSMA BETULINA (PILLANS) AND AGATHOSMA CRENULATA (PILLANS) FROM LOCAL PLANTINGS

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ABSTRACT

Measurements of leaf form from buchu plants collected in local plantings indicated that this criterion, the only taxonomic basis for distinguishing the two species, is a reliable method of identification but this does not hold true for hybrid buchu. G.L.C. and U.V. analysis of buchu oils showed that the presence of a relatively large percentage of ψ -diosphenol and diosphenol in A. betulina leaf oil only, is a valid criterion for botanically separating the two species. The analyses also showed that there is a wide variation in the percentage composition of the major components and in the percentage of oil obtained from different buchu plants.

UITTREKSEL

CHEMOTAKSONOMIESE IDENTIFIKASIE VAN DIE BOEGOE SPESIES AGA-THOSMA BETULINA (PILLANS) EN AGATHOSMA CRENULATA (PILLANS) UIT PLAASLIKE AANPLANTINGS

Boegoe-monsters is in drie plaaslike aanplantings versamel en visueel op grond van blaarvorm as rondeblaar, ovaalblaar en basters geklassifiseer. Die blaarmonsters is in die laboratorium gedroog en die oliedistillaat van elk, gaschromatografies en massaspektrometries analiseer; die U.V. spektra is ook bepaal. Die lengte/breedte verhouding van afsonderlike

blare per monster is ook bereken.

Die lengte/breedte verhouding van die blare is 'n betroubare maatstaf om die twee boegoe spesies te onderskei maar dit geld nie vir baster boegoe nie. Slegs rondeblaar boegoe (A. betulina) bevat die komponente \(\psi\-\)-diosfenol en diosfenol in redelike hoeveelheid en toon 'n U.V. piek by 272 nm. Ovaalblaar-boegoe (A. crenulata) toon 'n kenmerkende piek by 252 nm, te wyte aan pulegoon. Die teenwoordigheid van die twee diosfenole in rondeblaar boegoe is blykbaar 'n betroubare maatstaf om die twee spesies botanies te onderskei, maar dit geld nie in die geval van basterboegoe nie, wat ook die twee diosfenole, maar in kleiner hoeveelhede, mag bevat. Die hoof oliebestanddele van albei spesies is kwalitatief dieselfde maar toon groot kwantitatiewe verskille. Daar is ook relatief groot verskille in die persentasie olie wat van individuele plante verkry is.

INTRODUCTION

The natural habitat of the two commercially important buchu species *Agathosma betulina* and *A. crenulata* roughly extends from the Clanwilliam to Tulbagh, Paarl and Riversdale areas respectively. Taxonomically they are distinguished on the basis of leaf form only (Pillans, 1950). *A. betulina* is characterised by a smaller and rounded leaf shape as opposed to *A. crenulata* which has a larger oval-shaped leaf. This has been the basis of visual identification

Accepted for publication 12th October, 1975.

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used by growers and exporters and the two species are commonly known as round-leaf and oval-leaf buchu. However, since the establishment of buchu plantings in various parts of the Western Cape, a great deal of confusion as to the identity of these plants has arisen. Apparently a considerable amount of hybridisation has taken place over the years whenever the two species were interplanted and new plantings were established from seed collected in such plantings. Intermediate leaf forms are very common and the grower is faced with the problem of distinguishing between the two species. This is particularly important because overseas buyers prefer the round-leaf species which also fetches higher prices.

From a chemical point of view it has been known for some time that the essential oil produced from the dried leaves of A. betulina contains a considerable amount of diosphenol, the so-called buchu camphor. It has been shown by Fluck, Mitchell and Perry (1961) that an isomer of diosphenol, ψ -diosphenol, also occurs in A. betulina oil while A. crenulata oil contains only trace amounts of both components. The ultra-violet absorption spectrum of diosphenol and ψ -diosphenol are identical showing an absorbance peak at 272 nm (Fluck et al., 1961). They found that the oil of A. betulina also shows this characteristic peak thus providing a method of identifying this buchu species.

In an effort to identify the two buchu species, leaf samples were collected from established plantings and analyses of the oil distillates carried out by U.V. spectrophotometry and gas-liquid chromatography. Length/width ratios of leaf samples were also determined as a possible criterion of identity.

MATERIAL AND METHODS

Buchu leaf samples were collected during the summer from three plantings of growers in the Stellenbosch and Paarl area. The individual plants were visually classified as round, oval or intermediate (hybrid) according to leaf shape. The leaves were dried in an oven at 25°C and stored in air-tight glass containers at room temperature until analysed. The length and width of 20 leaves per plant were measured.

A ten gram leaf sample per plant to which 50 ml distilled water had been added, was water distilled for three hours in an all glass Karlsruhe* apparatus and the volume of oil obtained per sample was recorded. The U.V. absorption spectra of 2 mg of oil, taken up in 50 ml ethanol, were recorded on a Pye-Unicam spectrophotometer. The G.L.C. analyses were carried out with a Perkin-Elmer, Model-990 gaschromatograph. The recording conditions for the latter were as follows: Sample volume 1 μ l; injector temperature, 200°C,

^{*}Bender and Hobein, Karlsruhe, West Germany,

detector temperature 210°C; 38 cm \times 3,1 mm o.d. stainless steel column packed with 10% Carbowax 20 M on Chromosorb W/AW DMCS, 80–100 mesh; carrier gas-N₂; programme, 50°C to 150°C at 1°C per minute. The analyses were programmed to separate the main buchu oil components only. The relative percentage of each component per sample was estimated from the peak heights measured from a common base line. Peak height versus peak area i.e. peak height times width at half height showed such good correlation that it was possible to use peak height only. Identification of the components were made by direct coupling of the gas chromatograph to an AEI MS 902 mass spectrometer through a silicone membrane separator.

RESULTS

The results of analyses of buchu oil samples distilled from 24 individual plants are given in Table 1. It appears that pulegone is probably the most abundant constituent of the oil of both species followed by menthone and limonene which occur in approximately equal amounts. There is a striking variation between plants with regard to the percentage composition of the major components as shown by the C.V. values in Table 1. This has not been reported before as earlier analyses were apparently based on oil samples of commercial origin which are normally distilled from composite leaf batches exported from this country. The results confirm that ψ -diosphenol and diosphenol occur in round-leaf buchu only, whereas the other major components are qualitatively similar (See Fig. 1 and 2). The percentage ψ -diosphenol plus diosphenol (buchu camphor) in round-leaf buchu oil varies considerably and

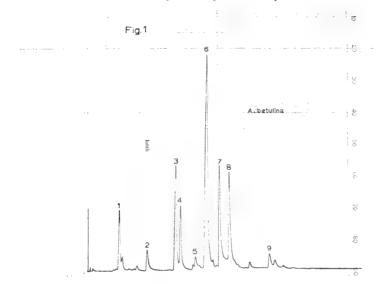
TABLE 1

Average values and coefficient of variation (CV) for the major oil components, oil content and length/width ratios of dried leaves from individual A. betulina (round leaf), A. crenulata (oval leaf) and hybrid buchu plants. (Transformed data (Arcsine) are given in brackets.)

Round leaf*		Oval leaf*		Hybrid**		LSD	
%	CV	%	CV	%	CV	(p=0,05)	
15,75	50,03	11,80	36,69	12,38	21,26	ns	
1,03	69,90	11,72	52,99	7,58	46,31	4,99	
21,32	27,30	12,65	24,90	14,48	29,70	5,39	
15,12	39,68	7,72	27,59	8,42	34,44	4,50	
2,45	65,31	4,55	6,37	4,42	21,04	1,25	
31,65	42,34	46,95	7,03	45,56	15,58	10,17	
5,08	95,08	0,00	0,00	1,93	227,98	7,27	
(11,96) 4,38	100,00	(0,00) 0,00	0,00	(3,70) 1,79 (2,10)	243,08	7,09	
3,15 2,53	77,78 34,78	4,65 2,38	21,19 22,27	3,74 2,43	27,54 25,10	ns ns 0,20	
	15,75 1,03 21,32 15,12 2,45 31,65 5,08 (11,96) 4,38 (11,92) 3,15	76 CV 15,75 50,03 1,03 69,90 21,32 27,30 15,12 39,68 2,45 65,31 31,65 42,34 5,08 95,08 (11,96) 4,38 100,00 (11,02) 3,15 77,78 2,53 34,78	76 CV % 15,75 50,03 11,80 1,03 69,90 11,72 21,32 27,30 12,65 15,12 39,68 7,72 2,45 65,31 4,55 31,65 42,34 46,95 5,08 95,08 0,00 (11,96) 4,38 100,00 0,00 (11,02) (0,00) 3,15 77,78 4,65 2,53 34,78 2,38	% CV % CV 15,75 50,03 11,80 36,69 1,03 69,90 11,72 52,99 21,32 27,30 12,65 24,90 15,12 39,68 7,72 27,59 2,45 65,31 4,55 6,37 31,65 42,34 46,95 7,03 5,08 95,08 0,00 0,00 (11,96) (0,00) 0,00 (11,92) (0,00) 0,00 3,15 77,78 4,65 21,19 2,53 34,78 2,38 22,27	% CV % CV % 15,75 50,03 11,80 36,69 12,38 1,03 69,90 11,72 52,99 7,58 21,32 27,30 12,65 24,90 14,48 15,12 39,68 7,72 27,59 8,42 2,45 65,31 4,55 6,37 4,42 31,65 42,34 46,95 7,03 45,56 5,08 95,08 0,00 0,00 1,93 (11,96) (0,00) (3,70) (3,70) 4,38 100,00 0,00 0,00 1,79 (11,02) (0,00) (2,10) (2,10) 3,15 77,78 4,65 21,19 3,74 2,53 34,78 2,38 22,27 2,43	% CV % CV % CV 15,75 50,03 11,80 36,69 12,38 21,26 1,03 69,90 11,72 52,99 7,58 46,31 21,32 27,30 12,65 24,90 14,48 29,70 15,12 39,68 7,72 27,59 8,42 34,44 2,45 65,31 4,55 6,37 4,42 21,04 31,65 42,34 46,95 7,03 45,56 15,58 5,08 95,08 0,00 0,00 1,93 227,98 (11,96) (0,000) (3,70) 438 100,00 0,00 1,79 243,08 (11,02) (0,000) (2,10) 3,15 77,78 4,65 21,19 3,74 27,54 2,53 34,78 2,38 22,27 2,43 25,10	

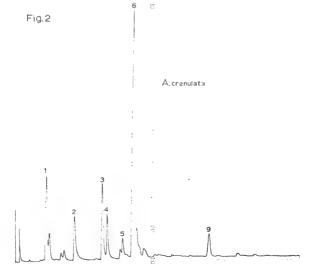
^{*}Mean of six plants

^{**}Mean of twelve plants



Representative gaschromatographs of *A. betulina* (Fig. 1) and *A. crenulata* (Fig. 2) leaf oils. Components:

1. Limonene, 2. Unidentified, 3. Menthone, 4. Iso-menthone, 5. Iso-pulegone, 6. Pulegone, 7. ψ -Diosphenol, 8. Diosphenol, 9. 8-Acetylthiomenthanone-3.



ranges from 28% to 2,7%. The two buchu species were also compared in terms of the new sulphur-containing compound, 8-acetyl-thiomenthanone-3, which is present in comparable concentration to the other major components. It appeared on the chromatogram at a retention time much higher than any other component hitherto identified. Identification was done by both mass spectrometer and NMR spectrometer. However, before this investigation had been completed a copy of a report by Kaiser, Lamparsky and Schudel (1973), was received in which the identification of this particular component had already been reported.

The U.V. absorption peaks also appear to be reliable criteria for identifying the two buchu species. All oil samples containing both diosphenols show a characteristic peak at 272 μm while the remainder show a peak at 252 μm . The latter is identical with that of pulegone which is the major oil constituent of both buchu species. The large variation in oil content between plants ranging from 4,0% to 1,4% is also of particular significance. The ratios of leaf length/width of round-leaf buchu significantly differed from those of both oval-leaf and hybrid buchu. For the latter two groups however, these ratios were not significantly different.

CONCLUSIONS

The taxonomic classification of the two buchu species A. betulina and A. crenulata is almost solely based on leaf form. In their natural habitat this criterion is probably valid. However, in present day plantings in which many progeny probably originated from hybrid seed, distinction of the two species on the basis of leaf form is often difficult. The results indicate that the ratios of leaf length/width is a most useful criterion for identifying the two buchu species. However such distinction is not valid between oval leaf and hybrid buchu and this is supported by chemical analyses of the oil indicating that hybrid buchu contains all the major components including the two diosphenols although the latter occur in considerably lower concentration. It is generally accepted that the qualitative composition of essential oils such as buchu leaf oil, is a specific property of the plant species in question although considerable quantitative differences may occur between particular individuals (Swain, 1966). In the case of the two buchu species therefore, it would appear that the most reliable criterion to identify round-leaf and oval-leaf buchu is the presence of ψ -diosphenol and diosphenol in the former. On the other hand it is also well-known that alterations in chemical components may often fall under specific genetic control and consequently hybridisation between the two buchu species could have led to variation in oil composition.

Commercially, buchu leaf oil is mainly used in the flavour and pharmaceutical industries and overseas buyers have always preferred the oil from round-leaf buchu probably because of its so-called buchu camphor content. It is not clear

whether the presence of the latter is important per se or is merely used to distinguish oil derived from the two species. The present analyses clearly show that in future it will be important to identify and propagate only those plants with a high oil content and in the case of round-leaf buchu, high diosphenol content as well. In this way, a more standardised product of high quality could eventually be made available to buyers and consumers. Several trials at this Institute have shown that buchu plants cannot be propagated vegetatively by cuttings. It will therefore be necessary to collect seed from chemically selected plants and propagate the progeny in isolated localities as a source of seed which can be made available to growers.

ACKNOWLEDGEMENT

The authors are indebted to Miss V. Truter of the Chemistry Department, University of Stellenbosch for carrying out the G.L.C. analyses.

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AN ANNOTATED LIST OF MICROFUNGI ISOLATED FROM THE SOILS AROUND PRETORIA, TRANSVAAL

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ABSTRACT

An ecological survey of soil fungi of an alkaline soil from an open-savannah in Transvaal was conducted over a period of one year. During this investigation numerous fungi were isolated by means of various isolation techniques. Descriptions of three of these species are given. Many of the fungi are new records for South African soil. An annotated list of all identified fungi is given in this report.

UITTREKSEL

'N LYS MET AANTEKENINGE VAN MIKROFUNGI GEÏSOLEER UIT DIE GRONDE OM PRETORIA, TRANSVAAL

'n Ekologiese opname van grondfungi van 'n alkaliese grond van die oop-savanna van Transvaal is uitgevoer oor 'n periode van een jaar. Tydens hierdie ondersoek is talryke fungi geïsoleer deur gebruik te maak van verskillende isolasietegnieke. Beskrywings van drie van hierdie spesies word gegee. Baie van die fungi is nuwe rekords vir Suid-Afrikaanse grond. 'n Geannoteerde lys van al die geïdentifiseerde fungi word in hierdie verslag gegee.

INTRODUCTION

Apart from the work of Papendorf and Von Arx (1966), Papendorf (1967, 1969), Papendorf and Du Toit (1967) and Eicker (1969, 1970 a & b) little is known about the microfungal populations of the local soils of natural communities. During an ecological survey of soil fungi of an open-savannah site in the Pretoria district of the Transvaal many fungi were isolated.

MATERIAL AND METHODS

The soil of the sampling area

The sampling site is situated in an undisturbed piece of Sourish Open-Savannah Veld (Acocks, 1953) with the dominant trees being *Celtis africana* Burm. f.; *Acacia caffra* (Thunb.) Willd. and *Diospyros lycioides* Desf. It occurs in the municipal area of Pretoria (25° 28° CA Pretoria) and receives an annual rainfall of 762,5 mm with the maximum precipitation during summer from November to February. The Daspoort Quartsite of the Pretoria Series yields a loam soil with a pH of 7,2.

Isolation techniques

Soil samples were collected at monthly intervals over a year commencing in May 1971. A sample of about 1 kg, comprising at least ten subsamples, was taken over an area of approximately 10m² using a sterile metal trowel. Samples were analysed within 24h of collection.

For the isolation of fungi three cultural methods were employed: the dilution plate method (Waksman & Fred, 1922) as modified by Menzies (1957), the soil plate method (Warcup, 1950) and a soil washing technique devised by Gams and Domsch (1967). For dilution plates Czapek-Dox-agar with 0,5% Difco yeast extract, rose bengal, $30~\mu g/ml$ streptomycin and $5~\mu g/ml$ aureomycin was used. The medium used both in the preparation of soil plates and in the washing technique was Peptone-dextrose agar plus rose bengal and the usual antibacterial agents (Martin, 1950). Isolation plates were incubated at 25° C and were periodically examined for at least three weeks in order to allow slow growing species to develop. Subcultures were grown on potato-dextrose or potato-carrot agar. Where growth on these media was unsatisfactory, 2% malt-extract agar or natural substrates such as sterilized grass debris were used. Penicillium and Aspergillus species were grown on Czapek-Dox-agar, while sterile mycelia were incubated under near-ultraviolet radiation (Leach, 1962) in an attempt to induce sporulation.

In the following list the numbers in brackets indicate the total number of times the fungus was isolated during the year of investigation; asterisks indicate that the species is a new record from South African soil; subcultures of fungi marked + have been deposited at the Commonwealth Mycological Institute, Kew.

OOMYCETES

Saprolegnia UP 812 (1). The only representative of the class. No special techniques, such as baiting, were employed for the isolation of the Saprolegniales.

ZYGOMYCETES

- ⁺Absidia cylindrospora Hagem (12). Although the species was isolated on several occasions it was not as common as in Zululand forest soils (Eicker, 1969).
- +Absidia spinosa Lendner (1).
 - Absidia UP 613 (1).
 - Actinomucor elegans (Eidam) Benjamin & Hesseltine (2)*.
- +Cunninghamella bainieri Naumov (1)*.
- +Cunninghamella echinulata (Thaxt) Thaxt ex Blakeslee (20). Occurred frequently, especially during autumn (April and May).
- +Congronelle butleri (Lendn.) Peyronel & Del Vasco (3).
- Mortierella UP 804 (1). I have commented previously on the relative scarcity of species of Mortierella in South African soils particularly in terms of the high percentage of occurrence of these fungi in European soils (Eicker, 1969).
- +Mucor fragilis Bainier (1)*.
- **Mucor spinosus van Tieghem (31)*. This was the most common example of the Zygomycetes.

 It was isolated in all samples throughout the study.
- +Mucor racemosus Fres (6)*.
- +Mucor UP 444 (1).
- Mucor UP 683 (1).

⁺Zygorhynchus moelleri Vuill (21). This homothallic species was characterized by the production of numerous zygospores in culture.

Sterile phycomycete UP 703 (1). Characterized by the production of robust, coenocytic hyphae.

ASCOMYCETES

The asocarp stages of *Penicillium* and *Aspergillus* have been classified with the rest of the species of these genera in the Deuteromycetes.

Achaetomiella irregulare D. Hawskw. ined (1)*. This new species also represents a first record of the genus for the African continent.

+ Auxarthron umbrinum (Boudier) Orr & Plunkett (4). See the taxonomic notes below.

+Chaetomium globosum (Kunze) Fr. (40). This perithecial fungus was the most common ascomycete, occurring regularly on isolation plates.

+Chaetomium globosum var. flavo-viride Novak (2).

Chaetomium lucitanicum Gomes (1)*.

+Chaetomium olivaceum Cooke & Ellis (1).

+Chaetomium spinosum Chivers (14). Isolated only during the dry, warm period (December and January).

+Chaetomidium subfimeti Seth (1). See the taxonomic notes below.

Cochliobolus spicifer Nelson (1).

+Nectria invectra Pethybr. (1).

Neocosmospora vasinfecta E. F. Smith (3). Neurospora sitophila Shear & Dodge (2).

+Pleospora infectoria Funckel (8). Only the Alternaria state of this species developed in culture. Thielavia terricola (Gilman & Abbott) Emmons (1).

BASIDIOMYCETES

Corticum (Rhizoctonia) solani Kühn (1). Although the basidiocarps of various Basidiomycetes were observed, especially from November to February, no special attempt was made to isolate these fungi from the soil.

DEUTEROMYCETES

Sphaeropsidales

⁺Coniella diplodiella (Speg.) Petrak & Sydow (7)*. This was the only pycnidial species which occurred with any noteworthy frequency.

+Coniothyrium fuckelii Sacc (1). Phoma UP 502 (1).

Phoma UP 819 (2).

Stagonospora UP 701 (1).

+Unidentified Sphaeropsidales UP 790 (1). Unidentified Sphaeropsidales UP 822 (3).

Melanconiales

Pestalotia UP 313 (1). Pestalotia UP 797 (1).

> Moniliales Moniliaceae

Aspergillus aculeatus Iizuka (2).
Aspergillus carneus (Van Tiegh.) Blochwitz (12). Isolated mostly during the summer (October - February).

+ Aspergillus flaviceps (Bain & Sart.) Thom & Church (1).

+Aspergillus flavus (Link) Fr. (8).

⁺Aspergillus fumigatus Fres. (10). Even though some of the isolation plates were regularly incubated at a higher temperature (45°C), A. fumigatus was the only thermophilic fungus isolated in this investigation.

+Aspergillus nidulans (Eidam) Wint (2).

⁺Aspergillus niger van Tiegh. (4). ⁺Aspergillus ochraceus Wilhelm (1).

+Aspergillus rugulosus Thom & Raper (54). This cleistothecial species produced prominent, dark brown Hülle cells and was very commonly isolated throughout the period of investigation.

+Aspergillus sydowii (Vuill.) Tiraboschi (1).

- +Aspergillus ustus (Bain.) Thom & Church (1). + Aspergillus versicolor (Vuill.) Tiraboschi (9). +Aspergillus wentii Wehmer (1)*. Aspergillus UP 410 (1). +Aspergillus UP 505 (1). Aspergillus UP 708 (1). Beauveria bassiana (Bals.) Vuill. (2). +Gliocladium roseum Bain, agg. (56), Isolated regularly throughout the investigation. +Gliocladium cf. roseum Bain, agg. (1). Gliocladium UP 629 (1). Monilia UP 727 (1). Paecilomyces UP 450 (28). Isolated periodically during the period of investigation. Paecilomyces UP 777 (7). Paecilomyces UP 797 (1). Paecilomyces UP 820 (1). +Penicillium brevicompactum Dierckx (1). +Penicillium canescens Sopp (2). +Penicillium chrysogenum Thom (8)*. +Penicillium crustosum (Thom) (1)*. +Penicillium cyclopium Westling (21). Common during early spring (August and September). +Penicillium decumbens Thom (1)*
- +Penicillium lilacinum Thom (1). +Penicillium multicolor G.M.-P. (58). This species was the most common and abundant fungus found in the alkaline soil under investigation. It was evidently not influenced by seasonal changes as it occurred on isolation plates of all soil samples throughout the year of investigation.
- +Penicillium rainstrickii Smith (10). +Penicillium thomii Maire (1)*. +Penicillium waksmanii Zal (7). +Penicillium UP 458 (1).

+Penicillium frequentans Westling (24). +Penicillium herqui Bain. & Sart. (2).

- +Penicillium UP 465 (1). +Penicillium UP 770 (2). This cleistothecial species showed very strong antagonistic properites on the isolation plates. Antibiotics produced by its colonies suppressed the growth of other isolates in its immediate vicinity very markedly.

+Penicillium UP 793 (1). +Scopulariopsis brevicaulis (Bain.) Thom (9).

Scopulariopsis UP 523 (1).

+Spicaria violaceae Abbott (44)*. Even though this fungus was isolated so abundantly from the Transvaal soil, this is the first record of the fungus for South African soil. +Trichoderma koningii Oud. (1).

+Trichoderma pseudokoningii Rifai agg (1).

+Trichoderma viride (Pers.) Gray (47). As is generally found, this species is one of the most common of soil fungi. Trichoderma UP 304 (1).

Verticillum UP 696 (2).

Dematiaceae

Acremoniella UP 373 (2). Alternaria alternata (Fr.) Keissler (1).

Alternaria tenuissima (Kunze ex Pers.) Wiltshire (5). Alternaria UP 462 (1).

+ Aurebasidium pullulans (de Bary) Arnaud (3). Cadosporium oxysporum Berk. & Curt. (2).

+Cladosporium tenuissimum Cooke (14). One of the few dematiaceous species that occurred quite frequently.

Cladosporium UP 428 (1). +Cladosporium UP 642 (1).

Gonytrichum macrocladum (Sacc.) Hughes (8)*.

Helminthosporium UP 662 (1).

Humicola fuscoatra Traaen (16). The most common representative of the Dematiaceae.

Humicola UP 721 (2). Mammaria UP 835 (1).

Periconia UP 496 (1).

Rhinocladiella cf. elatior Mangenot (1). See taxonomic notes below.

Stachybotrys atra Corda (7).

Torula UP 327 (1).

Trichocladium UP 852 (1)*.

Tuberculariaceae

Epicoccum purpurascens Ehrenb. ex Schlecht. (23). Isolated sporadically throughout the survey.

+Fusarium equiseti (Corda) Sacc. (3). +Fusarium graminearum Schwabe (8).

+Fusarium oxysporum Schlecht (23). By far the most common representative of the family and genus.

+Fusarium sambucinum Fuckel (2).

+Fusarium solani (Mart.) Sacc. (4).

Fusarium UP 326 (1). Fusarium UP 511 (1). +Fusarium UP 759 (2).

+Fusarium UP 761 (3).

Volutella ciliata (Alb. & Schw.) Fr. (2)*.

Stilbaceae

Doratomyces stemonites (Pers. ex Fr.) Morton & Smith (12).

+Graphium putredinis (Corda) Hughes (1)*.

Mycelia sterilia

Papulospora UP 517 (1).

Dark sterile mycelium UP 457 (46). Dematioid mycelia were quite common in the opensavannah soil with the type UP 457 being the most common. It could not be induced to sporulate.

TAXONOMIC NOTES ON SOME OF THE ISOLATES

Rhinocladiella cf. elatior Mangenot.

Vegetative growth rates on potato-dextrose agar, cornmeal agar and 2% malt-extract agar were 3,5; 1,5 and 1,4 cm in diameter respectively after three weeks of incubation at 25°C. The centre of the colony is raised, woolly and olivegray in colour. The margin of the colony is flat with appressed mycelium forming concentric rings. Reverse of the colony is dark olive-green. Sporulation is profuse on all these media.

Hyphae very regular, 1–2,6 μ m in diameter; no moniliform type seen. Hyphal stands rare. Conidiophores up to 85 µm long, lightly pigmented, forming branches which each terminates in a single, long, denticulate sporogenous tip, 4,5–9,7 μ m in length (Figure 1). Proliferation of the sporogenous cell occurs (Figure 2). Sporogenous cells are sympodulae with very pronounced scars in the spore bearing region (Figure 3). Blastospores produced singly from denticles, hyaline, long ellipsoid, 3,8–6,2 \times 1,2 \times 2,4 μ m, smooth.

As pointed out by Schol-Schwarz (1968), the production of phialospores occurs only rarely in some isolates. Hughes (1958) is of the opinion that those types having the *Phialophora* type of spore production should be placed in the genus Chloridium. No phialides were produced in the Transvaal isolate. This



Fig. 1. Rhinocladiella cf. elatior. A denticulate, sporogenous tip of a conidiophore. Note the scars in the spore bearing region. \times 1000.



Fig. 2. R. cf. elatior. A sporogenous cell showing proliferation. \times 1 000.



Fig. 3. R. cf. elatior. A scanning electron micrograph of a sporogenous cell showing the very pronounced scars left by conidia. × 12000.

species closely resembles R. elatior Mangenot but there are some differences mainly in cultural characteristics. The Transvaal isolate has a slower growth rate and more regular vegetative hyphae and there is no phialospore formation.

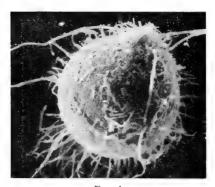
SPECIMEN EXAMINED

University of Pretoria 655 (I.M.I. 161, 683) isolated from alkaline soil, Pretoria, November 1971.

This is the first record of the occurrence of the species in South Africa.

Chaetomidium subfimeti Seth.

Colonies on 2% malt-extract agar spreading, light olive-brown. On potatodextrose agar a very thin, hyaline, spreading mycelium is formed. Perithecia abundant in old cultures, without ostiole or neck, globose, black, attached to the substratum by dark rhizoids (Figure 4). The perithecium is covered by dark brown appendages which are thick walled, roughened, swollen at the base, septate and unbranched with a somewhat hyaline, rounded tip. Asci club-shaped, 8-spored with spores irregularly biseriately arranged. Paraphyses rare, seen only in very young ascocarps, filiform, hyaline. Ascospores dark olive-brown, lemon-shaped, 8–11,5 \times 7–10,3 μ m. Apiculated at both ends (Figure 5).



Chaetomidium subfimeti. A perithecium, without ostiole, covered by unbranched appendages. S.E.M. × 220.

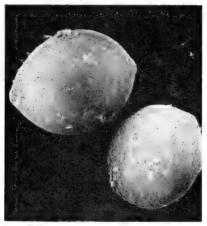


Fig. 5. C. subfimeti. Very characteristic lemon-shaped ascospores S.E.M. \times 4 500.

SPECIMEN EXAMINED

University of Pretoria 346 (I.M.I. 162, 626) isolated from alkaline soil, Pretoria, March 1972.

This isolate resembles most closely *C. subfimeti* as described by Seth (1967) but differs from it mainly in the somewhat larger ascospore size. The ascospores are, however, not large enough to warrant the inclusion of this fungus in *C. fimeti* Fuckel.

This is the first record of the occurrence of this genus in South Africa.

Auxarthron umbrinum (Boudier) Orr & Plunkett

Colonies on potato-carrot agar slow growing, granular, at first white, later turning yellowish brown. Underside of colony yellow to orange. A wine-red pigment diffuses into the medium. Ascocarps embedded in superficial mycelium, spherical, reddish-brown, diameter excluding appendages 150–460 μ m. Peridial hyphae yellow, 2,2–4,4 μ m in diameter, asperate (Figure 6) thick-walled, anastomosed dichotomously to form a reticulate peridium; septate with swollen knuckle joints measuring 4,4–6,1 μ m in diameter, ending in numerous short, roughened spinelike appendages with rounded or acute apices (Figure 7) or aseptate or with 1 or 2 septa, 3,3–69,0 μ m in length. Few elongate appendages, \pm smooth, sometimes branched, thick-walled, yellow-brown becoming discoloured towards an acute apex, aseptate except for one or two knuckle-joints near base, usually straight or apex slightly hooked, diameter at base 4,0–5,0 μ m and up to 860 μ m in length.

Asci hyaline, subglobose to ovoid, thin-walled, evanescent, 8 spored, 5,5–6,5 \times 6,5–7,6 μ m. Ascospores almost hyaline, smooth at all stages with a reticulate appearance, oblate, i.e. globose to subglobose from above and compressed in side view, 2,1–2,8 μ m, average 2,5 μ m in diameter (Figure 8). Asexual stage not observed.



Fig. 6.

Auxarthron umbrinum. Portion of a peridial hypha showing the asperate nature of its surface, S.E.M. × 12 500.

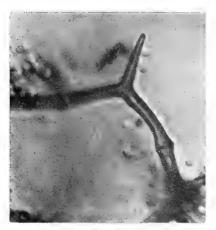


Fig. 7. A. umbrinum. A spinelike appendage in the region of a swollen knuckle joint of the peridial hyphae. \times 1 000.

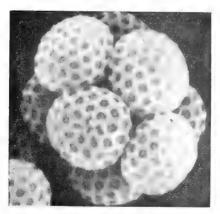


FIG. 8.

A. umbrinum. A group of eight ascospores showing the arrangement in an ascus. The spores are smooth and reticulate. S.E.M. \times 10 000.

SPECIMEN EXAMINED

University of Pretoria 433 (I.M.I. 164, 235). Isolated from alkaline soil, Pretoria, August 1971.

This isolate is most similar to A. umbrinum as described by Orr, Kuehn and Plunkett (1963) and also to an isolate of the same species described by Papen-

dorf (Marasas et al., 1966) from litter of Acacia karroo in Transvaal. The isolate differs from previous descriptions of A. umbrinum mainly in the ascospores being at all times smooth and reticulate, the maximum diameter of the ascocarp and of the ascospores, and the infrequent branching of shorter appendages. An interesting characteristic which has not previously been reported for these fungi is the presence of branched, elongate appendages.

Apinis (1964), in his revision of the British Gymnoascaceae, placed this species in the genus Gymnoascus (subgenus Auxarthron). Most modern authors retain the genus name Auxarthron (Von Arx, 1970; Ainsworth, Sparrow & Sussman, 1973).

ACKNOWLEDGEMENTS

The author wishes to thank Dr. P. M. Stockdale of the C.M.I., Kew and Dr. Arvids E. Apinis of B.R.U. Merioneth, Wales for their comments on some of the isolates. The financial assistance of the C.S.I.R., Pretoria and the Research and Publications Committee of the University of Pretoria is gratefully acknowledged. I wish to thank Prof. H. P. van der Schijff for continued encouragement.

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SHORT COMMUNICATION

THE IDENTITY OF PROTEA MAGNIFICA LINK

J. P. ROURKE

(Compton Herbarium, Kirstenbosch)

ABSTRACT

Protea magnifica Link (1821) antedates the name Protea barbigera Meisn. (1856).

UITTREKSEL

DIE IDENTITEIT VAN PROTEA MAGNIFICA LINK

Protea magnifica Link (1821) 'n vroeëre naam vir Protea barbigera Meisn. (1856) word aangeteken.

INTRODUCTION

In 1821, Dr H. F. Link published a catalogue of the plants growing in the Royal Botanic Garden, Berlin. This list enumerates eleven species of *Protea*, of which only one, *Protea magnifica*, was described by Link as new. Apart from a brief diagnostic description, Link cites plate 438 in H. C. Andrews's *Botanisi's Repository*, in his account of *P. magnifica*. Since no type material of *P. magnifica* has survived at Berlin (B), if indeed any was ever preserved in the first place, plate 438 in Andrews's *Botanisi's Repository* must serve as the lectotype of the name. Significantly, Phillips and Stapf upheld *P. magnifica* Link in the *Flora Capensis*, but cited no collections under this name as they apparently were unable to associate any herbarium material with the plant depicted in Andrews's plate.

INTERPRETATION OF ANDREWS'S PLATE

Andrews's plate is a life size illustration of a flowering specimen from George Hibbert's collection. As is so often the case with Andrews's illustrations, it is rather stylized which is, perhaps, why Phillips and Stapf were unable to associate this plate and its accompanying description with any herbarium material. Here is another case where it is only too clear that had Phillips and Stapf been well acquainted with living material of *Protea* they would have been much better able to interpret some of the rather artless illustrations of Proteas prepared from plants grown under glasshouse conditions in Europe during the 18th and 19th centuries.

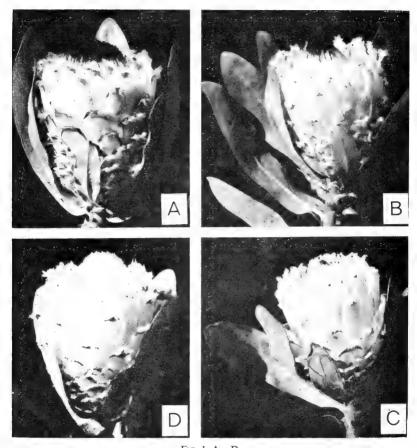


FIG. 1, A – D

Protea magnifica Link, showing the presence or absence of a dome of black pubescence in the centre of newly opened inflorescences, as well as variation in the size of the dome of black pubescence.

Specimens A – D are from a population sampling on Jonaskop, Riviersonderend mountains (*Rourke* 1492 (NBG)).

In fact, the species depicted in Andrews's plate 438 is conspecific with *Protea barbigera* Meisn. The specimen illustrated has a fully expanded inflorescence with the involucral bracts widely splayed as is typical in the post anthesis phase. It shows a form of this species having cream involucral bracts and no central dome of black pubescence. This form, lacking the central dome of black

pubescence, while unusual, is well within the normal range of variation in this species. As an example, a selection of specimens having creamy-green involucral bracts was collected from a population on Jonaskop in the Riviersonderend mountains (Fig. 1, A - D). At this locality, as at many others, there is considerable variation in the size and form of the central dome of black pubescence and in some plants the black dome is altogether absent (Fig. 1, D). This latter specimen matches Andrews's plate 438. Moreover, the dissected floral parts at the base of plate 438 show the characteristic white plumed awns on the adaxial perianth sheath and the abaxial perianth segment. Also, the form, dimensions, colour and pubescence of the leaves are quite distinctly diagnostic. In conclusion, it is worth quoting part of Andrews's description which accompanies plate 438:

"the upper scales of the empalement (i.e. the involucre) are lance-shaped, bearded, and of a yellowish white: the scales beneath are broadly ovate, downy, bearded, and discoloured towards the ends."

Such a description can only fit the cream-coloured form of the species hitherto known as *Protea barbigera* Meisn. As *Protea magnifica* Link (1821) antedates *Protea barbigera* Meisn. by 35 years, the familiar name *Protea barbigera* must now go into synonymy and *Protea magnifica* must be upheld as the correct name for this species. Although the earliest available name, *Erodendrum magnificam* Salisb. ex Knight (1809) is based on the same iconotype as *Protea magnifica* Link (1821), Link did not transfer Knight's epithet *magnificum* to *Protea*.

SYNONYMY

Protea magnifica Link, Enum. Plant. Berol. (1): 113 (1821); Phill. & Stapf in Fl. Cap. 5:570 (1912). Type: Andr., Bot. Rep. t. 438 (Dec. 1806).

Erodendrum magnificum Salisb. ex Knight in Knight, Cult. Prot.: 37 (1809). Type: Andr., Bot. Rep. t. 438 (Dec. 1806).

Protea barbigera Meisn. in DC., Prodr. 14: 233 (1856); Phill. & Stapf in Fl. Cap. 5:563 (1912); R. A. Dyer in Flower Pl. Afr. 28: t. 1086 (1950); Rousseau, Prot. of S.A. 19 – 24 (1970). Syntype: In rupestribus Witzenberg Zeyher s.n. in herb. Meisn. (NY!).

THE STATUS OF OCHTODES CAPENSIS (J. AGARDH) J. AGARDH (RHIZOPHYLLIDACEAE, GIGARTINALES, RHODOPHYTA)

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ABSTRACT

Evidence is presented that suggests that the red alga *Sphaerococcus capensis* J. Agardh = *Ochtodes capensis* (J. Agardh) J. Agardh was erroneously reported from the Cape of Good Hope and that this species should be placed in synonomy under the Western Atlantic taxon *Ochtodes secundiramea* (Montagne) M. A. Howe.

UITTREKSEL

DIE STATUS VAN *OCHTODES CAPENSIS* (J. AGARDH) J. AGARDH (RHIZO-PHYLLIDACEAE, GIGARTINALES, RHODOPHYTA)

Bewyse word aangelewer dat die rooi alga Sphaerococcus capensis J. Agardh = Ochtodes capensis (J. Agardh) J. Agardh verkeerdelik aangemeld was vanaf Kaap Die Goeie Hoop en dat die soort as 'n sinoniem geplaas behoort te word onder die Wes-Atlantiese takson Ochtodes secundiramea (Montagne) M. A. Howe.

Introduction

The marine algal flora of South Africa has long been of especial interest to phycologists because of its richness and diversity. A measure of the intensity of this interest may be gained by a perusal of a guide to the literature of the marine algae of this region compiled by Seagrief and Troughton (1973). The status of a species originally described by J. Agardh (1852) from the Cape of Good Hope as *Sphaerococcus capensis* and then transferred by Agardh (1872) to the genus *Ochtodes* as *O. capensis* is reviewed.

HISTORICAL RÉSUMÉ

When J. Agardh (1872) established the genus Ochtodes, he based his concept of the genus on three taxa: O. filiformis (J. Agardh) J. Agardh from Martinique in the West Indies; a variety of this species from St. Barthélemy given the varietal epithet cervicornis by Agardh; and Ochtodes capensis. The generic name, derived from the Greek ochthodes which means humped or warted, was chosen by Agardh because of the prominent cystocarpic protuberances of the variety. Agardh (1852) had previously placed the above cited species with doubt into the genus Sphaerococcus sensu Greville as S. filiformis J. Agardh and S. capensis because the variety was apparently not available to him at this time and the two species did not have distinguishing reproductive features to separate them from

Sphaerococcus. His separation of these two species was based on differences in branching patterns.

Schmitz (1889) recognised J. Agardh's erection of the genus *Ochtodes* as a separate taxon and, since there was no generic holotype, he made *O. filiformis* (J. Agardh) J. Agardh the lectotype. Howe (1920) found that *O. filiformis* is a later homonym of *O. secundiramea* (Montagne) Howe and is, therefore, illegitimate and cannot serve as the type of the genus. The family to which *Ochtodes* has traditionally been assigned, the Rhizophyllidaceae, has been recognised as a member of the Cryptonemiales, however, based on the non-accessory nature of the auxiliary cell branch, Wiseman (1975) has transferred the family to the Gigartinales.



Fig. 1.

Type specimen of Sphaerococcus capensis J. Agardh=Ochtodes capensis (J. Agardh)

J. Agardh in the Agardh Herbarium (No. 27121) at Lund. Scale 1 cm.

Agardh's original description of *Sphaerococcus capensis* was based on a specimen (or specimens?) sent to him by the brothers Crouan. Since Agardh did not indicate the collector, and the type specimen (Fig. 1) and only specimen of this species in the Agardh Herbarium (No. 27121) is without collection data beyond Table Bay, the Cape of Good Hope inscribed in French by one of the Crouans, the collector remains unknown. The Crouans apparently did not collect outside of Brittany (Dixon, 1967).

Picquenard (1912), who compiled a catalogue of the specimens in the Crouan herbarium at Concarneau, referred to a single specimen of *O. filiformis* which he identified, but he made no reference to *O. capensis*. Picquenard noted that the collector and locality of the specimen was unknown, and that he assumed that it was from the West Indies. Not having seen this specimen, I would hesitate to suggest that it came from the original material upon which Agardh made his circumscription of *O. capensis*, nevertheless, since the specimen at Concarneau is without collection data, and the data of the specimen of *O. capensis* at Lund was inscribed by one of the Crouans, this does raise the possibility that the Crouans might have inadvertently written the wrong locality on the specimen that they sent to Agardh.

There is no published record of *O. capensis* having been recollected and identified as this species from South Africa. Dr. G. F. Papenfuss (personal communication) has informed me that Table Bay is one of the more heavily collected sites in South Africa. The fact that this species ostensibly has not been reported again from South Africa does not preclude the possibility that it has been recollected but remains unidentified or misidentified. This seems unlikely because the double-helicoid biaxis of the genus is so striking and unique within the red algae that identification is not difficult. More than likely, the specimen sent to Agardh by the Crouans was collected in the West Indies by Mazé and Schramm and forwarded to the Crouans who were responsible for making many of the determinations for these collectors.

PRESENT STATUS

The type specimen, and possibly the only extant specimen annotated as Sphaerococcus capensis and Ochtodes capensis, is spermatangial and has the unique biaxial structure of the genus Ochtodes. Agardh observed the axial structure of this species, but did not comment on the spermatangial branches which are difficult to distinguish from outer cortical cells. In Ochtodes the spermatangial branches collectively form a nemathecium. The dimensions of these branches in the type specimen of O. capensis do not differ from the dimensions of the same branches of O. secundiramea. The congested, corymbose branching pattern of the type specimen of O. capensis does not differ from the branching pattern of many specimens of O. secundiramea from the Western Atlantic.

The morphological evidence as well as the historical ambiguities surrounding O. capensis, suggests that this species be recognised as being conspecific with O. secundiramea, and, accordingly, should be placed in synonomy under the latter species. This decision appears to be the most judicious one at this time, but if tetrasporangial and/or female plants are recollected from South Africa, the conspecificity of the two taxa will have to be re-evaluated.

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THE PREPARATION OF 2,3 (3H)-GA₂₉ AND ITS METABOLISM BY ETIOLATED SEEDLINGS AND GERMINATING SEEDS OF DWARF PISUM SATIVUM (METEOR)

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ABSTRACT

(3H)-GA₂₉ was prepared biosynthetically from (3H)-GA₂₀ by germinating pea seeds. (3H)-GA₂₀ applied to dark-grown seedlings and germinating seeds of dwarf Pisum was converted into polar, acidic products, but analysis of these products by mass spectrometry was rendered impossible by low levels of metabolites, and a lack of unlabelled GA₂₉ with which to increase metabolite pool-sizes. The results are discussed in relation to recent attempts to investigate the pathways of gibberellin biosynthesis in higher plants, and to draw attention to some of the problems associated with these investigations.

UITTREKSEL

DIE BEREIDING VAN 2,3 (3H)-GA29 EN DIE METABOLISME DAARVAN DEUR GEËTIOLEERDE SAALLINGE EN ONTKIEMENDE SADE VAN DWERG *PISUM*

SATIVUM (METEOR)

(3H)-GÀ₂₉ is biosinteties van (3H)-GA₂₀ voorberei deur ertjiesade te ontkiem. (3H)-GA₂₉ toegedien aan in die donker gekweekte saailinge en ontkiemende sade van dwerg *Pissum* is verander tot polare suurvormendeprodukte maar ontleding van die produkte deur massa spektrometrie was onmoontlik weens die lae vlakte van metaboliet en die afwesigheid van ongemerkte GA₂₉ om die metabolietpoel te vergroot. Die resultate word bespreek in die lig van die jongste pogings om die gibberellien biosintese roete in hoër plante na te speur en om die aandag op sekere probleme verbonde aan hierdie navorsing, te verlig.

INTRODUCTION

Studies have recently been conducted to elucidate the pathway(s) of gibberellin (GA) biosynthesis in intact seedlings of dwarf *Pisum* (Durley, Railton and Pharis, 1973; Durley, Railton, and Pharis, 1974, 1975; Railton, Durley and Pharis, 1974a, 1975a; Railton, Murofushi, Durley and Pharis, 1974b). Preliminary studies were of a somewhat exploratory nature and utilised some labelled precursors and intermediates which were not known to be native pea GAs. Thus, 1,2 (³H)-GA₅ and 1,2 (³H)-GA₁, two GAs believed on circumstantial evidence, to be native to dwarf pea (Kende and Lang, 1964), were converted respectively, to GA₃ (Durley *et al.*, 1973) and the diol, GA₈ (Railton, Durley and Pharis, unpublished data). Similarly, 16, 17 (³H)-GA₁₄, an early intermediate in the GA biosynthetic pathway in the fungus, *Gibberella fujikuroi*

(Cross et al., 1968), was metabolised by etiolated dwarf pea seedlings to GA_{18} , GA_{38} , GA_{23} , GA_{1} , GA_{3} (Durley et al., 1974, 1975) and a new GA, GA_{14} -hydrate (Durley et al., 1975) which has recently been isolated from G. fujikuroi and allocated the "A" number, GA_{42} (Bearder and MacMillan, 1973).

Concurrent with metabolism studies, attempts were made to investigate the GA content of the pea seedling. It had previously been assumed that pea seedlings contained only 2 GA-like substances, one similar to GA₃ and/or GA₁, and the other similar to GA₅ and/or GA₂₀ (Kende and Lang, 1964; Jones and Lang, 1968). A reinvestigation of this work using different analytical techniques. indicated the presence of at least 6 GA-like substances in pea seedlings, one of which was similar to GA_a (Railton and Reid, 1974; Railton, Durley and Pharis, unpublished data, 1972). In parallel studies, MacMillan and co-workers have recently investigated the GA content of immature seed of dwarf pea and have characterised, by combined gas chromatography-mass spectrometry (GC-MS), GA₉, GA₁₇, GA₂₀, GA₂₉, GA₃₈, and 13, hydroxy-GA₁₅, as native pea GAs (Frydman and MacMillan, 1973; Frydman et al., 1974). The GA, 13, hydroxy-GA₁₅ was previously synthesised from GA₁₉ by borohydride reduction (Fukuii et al., 1972) and has now been allocated the "A" number GA₄₄ (Frydman et al., 1974). Application of 16, 17 (3H)-GA9 to inact dwarf pea seedlings, showed it was converted into GA₂₀ (I), GA₂₉ (II), the hitherto unknown GA, 2,3 dihydro-GA₃₁, and the hydrate of GA₉, GA₁₀ (Railton et al., 1974a, 1975a). When 2,3 (3H)-GA₂₀ was fed to dwarf pea, it was hydroxylated, specificially, at C-2 to produce GA29 in high yield (Railton, Murofushi, Durley and Pharis, 1974b).

The demonstration that GA_9 is converted via GA_{20} to GA_{29} , indicates that these 3 GAs form part of a biosynthetic sequence in the pea plant. Furthermore, the presence of GA_{17} , GA_{38} and GA_{44} suggests the existence of more than one GA biosynthetic pathway in dwarf *Pisum*. In order to investigate further the biosynthesis of GAs in *Pisum*, it is necessary therefore, to produce in labelled form, other native pea GAs. Difficulties in total chemical synthesis and the unavailability of many GAs in reasonable quantities has limited the production of radioactively labelled GAs. In the present paper, the biosynthetic preparation of 2,3 (3 H)-GA $_{29}$ of high radionuclidic purity is reported and preliminary attempts described to study its metabolism in dwarf *Pisum sativum*.

MATERIAL AND METHODS

Synthesis of 2,3 (3 H)-GA $_{20}$. This was prepared by the method of Murofushi et al., (1974). Gibberellin A $_{5}$ was converted into its methyl ester with ethereal diazomethane and then treated with meta chloroperbenzoic acid to afford the epoxide of GA $_{5}$ methyl ester. Reduction of this epoxide with tritium yielded 2,3 (3 H)-GA $_{20}$ methyl ester epoxide. Cleavage of the epoxide ring was achieved with

iodine and zinc dust and the ester hydrolysed with 0.2N sodium hydroxide to afford 2,3 (^{3}H)- GA_{20} , sp. act 2.0 Ci/mM.

Preparation of 2,3 (3 H)-GA₂₉. Dry, mature seeds of dwarf Pisum sativum L. (Meteor) were imbibed in distilled water containing 10 μ Ci (0.6 μ g) 2,3 (3 H)-GA₂₀ under continuous illumination at 22°C. A total of 15 seeds were used and following radical emergence, were ground in a mortar with acid-washed sand and chilled 80% methanol. All methanol was removed *in vacuo* at 35°C, the remaining aqueous phase adjusted to pH 9.0 with an equal volume of 0.5M

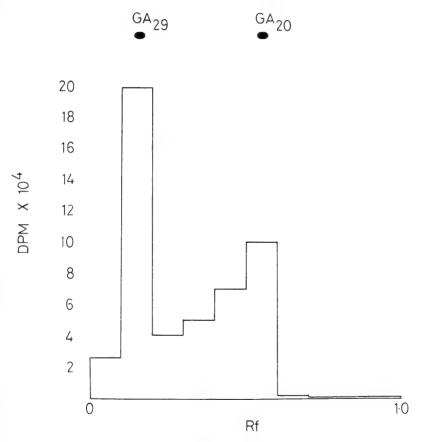


Fig. 1 Preparation of (3 H)-GH $_{29}$ and its metabolism in dwarf *Pisum*.

phosphate buffer (pH9.0) and partitioned against diethyl ether to remove basic/neutral impurities. The acqueous phase was then adjusted to pH 3.0 with IN HCl and partitioned 6X against ethyl acetate. The ethyl acetate fraction was reduced to dryness in vacuo and the residue chromatographed on preparative TLC using silica gel H and the solvent system ethyl acetate, chloroform, formic acid (50:50:1, v/v). A single zone of radioactivity (Rf 0.1–0.2) corresponding to a marker of authentic GA_{29} (Figure 1) was eluted with water-saturated ethyl acetate and then reduced to dryness.

PURIFICATION

(i) *PVP column chromatography*. The eluate from the TLC plates was purified further by column chromatography using insoluble poly-N-vinyl pyrrolidone (PVP) eluted with 0.1 M phosphate buffer, pH 8.0 (Glenn *et al.*, 1971).

(ii) Silica gel partition column chromatography. GA_{29} recovered from the PVP column was finally purified by high efficiency silica gel partition column chromatography using a modification of the method of Powell and Tautvydas (1967). This was carried out as follows: silica gel (Mallinkrodt CC4, for column chromatography) was dried to constant weight in an oven and then slurried with a calculated amount of 0.4M formic acid until the gel had the consistency of moist sand. After leaving to equilibrate for 4 days, the liquid coated support phase was slurried in formic acid-saturated n-hexane and degassed under vacuum. The column was packed in n-hexane in a nitrogen enriched atmosphere to minimise air uptake by the solvents during packing. Failure to do this results in partial "stripping" of the liquid stationary phase during chromatography

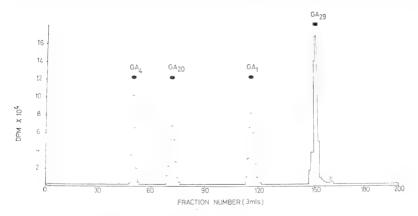


Fig. 2
Preparation of (3H)-GA₂₉ and its metabolism in dwarf *Pisum*.

with marked reductions in column efficiency (Kirkland, 1971). The partially purified radioactive GA_{29} sample was introduced on to the top of the column in 100 μ L of ethyl acetate and the column eluted with n-hexane containing increasing percentages of ethyl acetate. GA_{29} eluted as a discrete peak (Figure 2) which was collected, reduced to dryness and an aliquot taken for analysis by gas liquid-radiochromatography (GLRC).

(iii) Gas liquid-radiochromatography. GLRC analysis was carried out in a similar manner to that described previously (Durley et al., 1973; Durley et al., 1974, 1975, Railton et al., 1974a). 2,3 (3H)-GA₂₉ methyl ester, trimethylsilyl ether chromatographed as a single peak on GLRC, viz.: 2% QF-1 (205°), 13.5 min; 1% XE-60 (207°C) 15.3 min; 2% SE-30 (203°C), 16.9 min; with identical retention times to those of an authentic sample of derivatised GA₂₉, viz.: 2% QF-1 (205°C) 13.5 min; 1% XE-60 (207°C), 15.3 min; 2% SE-30 (203°C), 16.8 min.

2,3 (3H)-GA₂₉ was stored in 95 % ethanol at -20°C.

Application to dwarf pea and extraction. 2,3 (3 H)-GA $_{29}$ (2.5 \times 10 5 dpm) was applied in 5 μ l droplets of 50% ethanol to the plumular hook of 5 day old etiolated pea shoots or dissolved in distilled water and dry, mature seed allowed to imbibe until the radicle had broken through the seed coat. Etiolated shoots were harvested 22 hr. after (3 H)-GA $_{29}$ application and seeds after 48 hr. Tissues were ground in 80% methanol and extracted as described above under *Preparation of* 2,3 (3 H)-GA $_{29}$, except that the aqueous phase remaining after ethyl acetate extraction was further partitioned against n-butanol at pH 3.0. The acidic ethyl acetate fraction was chromatographed on thin layers of silica gel G using ethyl acetate, chloroform, formic acid (50:50:1 v/v), the gel scraped directly into scintillation vials, eluted with absolute methanol and levels of radioactivity measured in a Packard Tricarb scintillation spectrometer fitted with an absolute activity analyser. Toluene containing 2,4-diphenyl oxazole (5 g/L was used as scintillant).

RESULTS AND DISCUSSION

Gibberellin A_{20} was converted into GA_{29} in yields of 30–40 percent by germinating pea seeds. This is an exceptionally high percentage conversion, probably the highest yet recorded for an intact organ of a higher plant. Most previous studies employing radioactive GAs have achieved conversions in the order of 1–5 percent (see Musgrave and Kende, 1970; Durley *et al.*, 1974).

In previous studies (Railton et al., 1974a) it was found that etiolated shoots of dwarf pea converted GA₂₀ into GA₂₉ less efficiently than did germinating seed; conversions of GA₂₀ in shoots being in the order of 3–4 percent. This suggests that marked differences exist between organs of dwarf pea in their ability to metabolise GAs.

The build-up of GA_{29} in seed compared to shoot, could indicate either, a more active $2,\beta$ -hydroxylase enzyme in seed which converts $GA_{20} \rightarrow GA_{29}$, or, a more efficient system in seedlings which metabotises GA_{29} and prevents its

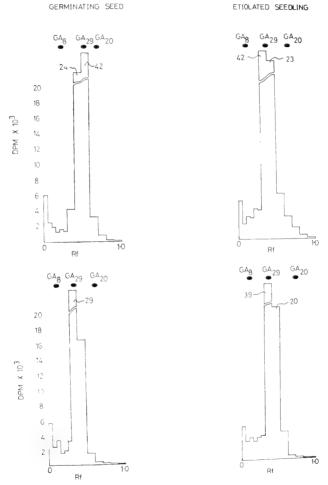


Fig. 3 Preparation of (3H)-GA $_{29}$ and its metabolism in dwarf Pisum.

Germinating Etiolated seed seedling

accumulation. Radioactive GA_{29} was therefore prepared biosynthetically to help resolve this problem.

2,3 (³H)-GA₂₉ was converted into a similar spectrum of acidic, radioactive metabolites by both etiolated seedlings and germinating seeds of dwarf *Pisum*. The results of 2 separate experiments are shown in Figure 3. Two main zones of radioactivity were observed; an extremely polar zone (Rf 0.0–0.1) and a less polar zone exhibiting similar chromatographic properties to those of GA₈ (Rf 0.15–0.26). A third zone was also detected which was poorly resolved from GA₂₉ itself, particularly in extracts of seed. GA₂₉ was converted into the most polar zone in yields of 1.5–2.0 percent by germinating seeds and in yields of 0.8–1.0 percent by seedlings. The less polar zone was produced from GA₂₉ in percentage conversions of 0.7–1.0 percent by seeds and 0.4–0.9 percent by seedlings.

The similar chromatographic behaviour of one of the polar metabolites to that of GA₈ suggests that GA₂₉ might be hydroxylated at C-3 to produce this diol. However, it has already been shown in dwarf pea that GA1, in which C-3 is already hydroxylated, is specifically converted by 2, β -hydroxylation to GA₈ (Railton, Durley, and Pharis, unpublished data). It thus seems unlikely therefore, that GA₈ is indeed produced from GA₂₉. However GA₁ has not, as yet, been detected in dwarf pea (MacMillan, personal communication) and the significance of the conversion of $GA_1 \rightarrow GA_8$ could be questioned, although the dangers inherent in drawing conclusions from negative data are wellknown. Further, the orientation of tritium atoms at the C-2, C-3 double bond in GA₂₀ is not known and introduction of [OH] at these sites might result in complete displacement of tritium and an inability to detect GA8. The nature of the very polar metabolite remaining on the origin of chromatograms (Rf 0.0-1.1) is unknown. A similar metabolite zone was detected amongst the conversion products of GA₉ in dwarf pea (Railton et al., 1974) but all attempts to characterise it by GC-MS have so far failed (Railton, Durley and Pharis, unpublished data). The distribution of radioactivity between the diethyl ether, ethyl acetate and n-butanol fractions is shown in the Table. Interestingly, the n-butanol fractions from both seed and seedlings contained significant levels of radioactivity, suggesting conversion of GA₂₉ and/or its metabolites to very polar compounds such as GA-glycosides. GA_{20} –2–0– β –D–glucopyranosyl ether has been isolated from a higher plant source (Yokota et al., 1970).

In previous work, the highly successful technique of applying "cold carrier" along with the radioactive GA led to the unequivocal characterisation of radioactive GA metabolites in dwarf *Pisum* by GC-MS (Railton, *et al.*, 1974 a, b; Durley *et al.*, 1975; Railton *et al.*, 1975a). In the present work the unavailability of GA_{29} in reasonable amounts hampered any attempts to increase GA_{29} metabolite "pool" sizes and so obtain enough mass of product for detailed

spectral analysis. It is obvious that future biosynthetic studies in higher plants involving the use of rarer GAs will be greatly impeded until methods have been devised for the chemical synthesis of these GAs.

TABLE Distribution of radioactivity between the diethyl ether, acidic ethyl acetate and n-butanol fractions from extracts of seed and etiolated seedlings of dwarf $Pisum\ sativum\ treated$ with (^3H) - GA_{20}^+ .

Expt. No.	Diethyl ether (dpm)	SEED Ethyl acetate (dpm)	n-butanol (dpm)	Diethyl ether (dpm)	SEEDLING Ethyl acetate (dpm)	n-butanol (dpm)
(1)	0	8,7 x 10 ⁴	1,2 x 10 ³	0	9,7 x 10 ⁴	6,0 x 10 ³
(2)	0	6,6 x 10 ⁴	6,0 x 10 ²	0	8,4 x 10 ⁴	2,2 x 10 ³

*2,5 x 105 dpm per treatment

The present results show that GA_{29} was metabolised to a similar extent in both germinating seed and etiolated seedlings of dwarf pea. This would suggest therefore that germinating seeds possess a more active $2,\beta$ -hydroxylase enzyme system than etiolated shoots rather than a less efficient method for removing accumulating GA_{29} . Recent work in this department has resulted in the isolation of a $2,\beta$ -hydroxylase from germinating pea seeds and its properties are currently under investigation.

The problem of differences in percentage conversions of applied radioactive GAs is interesting. The significance for example, of a 1.5–2.0 percent conversion of GA_{29} into its most polar metabolite in 24 hours, could be questioned as not being particularly meaningful from a biosynthetic point of view. However, GA_{29} is a native pea GA and it would be expected that the plant would possess the ability to metabolise it efficiently. Apparent low conversion percentage conversions of GAs to their metabolites could be due to two main factors.

- (1) Permeability restrictions allowing only a small percentage of the applied precursor to reach the actual site of interconversion. This could mean that a 2,0 percent conversion based upon the amount of precursor supplied, could represent a 100 percent conversion as far as the plant is concerned.
- (2) Most of the applied precursor reaches the site of interconversion but the plant carefully controls the "pool size" of the metabolites, allowing say, only 2.0 percent of the applied precursor into the "pool" at any time. This suggests that "turnover rates" of GAs and their precursors are subject to fine control mechanisms, a possibility which, on present evidence, cannot be dismissed. In relation to this possibility, time course studies

using the GA precursor *ent*-Kaurenoic acid applied to dwarf rice seedlings showed that the levels of this compound decreased with time and yet were unaccompanied by significant increases in levels of its metabolites (Railton *et al.*, 1975b) suggesting regulation of metabolite "pool" sizes.

This means that quoting a percentage conversion for an applied radioactive GA only indicates the amount of product in any "pool" at any one time and is therefore not a true indication of how much GA has actually been metabolised. More satisfactory data could be achieved therefore, if the "turnover" rates of individual GAs could be determined. Preliminary attempts have been made to investigate "turnover" rates of GA₂₀ in dwarf *Pisum* (Railton, 1974 a, b) and, although not fully satisfactory at the present time, they offer a method of obtaining more meaningful information regarding the metabolism of labelled GAs in higher plants.

The present results indicate that germinating pea seeds metabolise different GAs in a biosynthetic sequence at different rates and mechanisms must therefore exist to control these rates of metabolism. The rapid accumulation of GA₂₉, a GA exhibiting low biological activity, suggests that pea seeds possess a mechanism for the efficient, deactivation of biologically active, GA₂₀. The significance of this remains to be determined.

$$CO$$
 H
 CO_2H
 $CO_$

Fig. 4 Structures of GA_{20} and GA_{29} . Preparation of (3H)- GA_{29} .

ACKNOWLEDGEMENTS

I wish to thank Dr. D. Broadbent, Pharmaceuticals Division, I.C.I. Limited, Alderley Park, Cheshire (U.K.) for supplying GA₅, Dr. J. MacMillan, School of Chemistry, University of Bristol (U.K.) for GA₈, Dr. Noboru Murofushi and Professor N. Takahashi, Department of Agricultural Chemistry, University of Tokyo, Japan, for samples of GA₂₀ and GA₂₉ and for details of the synthesis of 2,3 (³H)-GA₂₀, and Dr. Alan Crozier, Botany Department, University of Glasgow (U.K.) for details of the modified silica gel partition column.

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SOME OBSERVED INTERRELATIONSHIPS BETWEEN THE COVER OF AQUATIC VEGETATION AND VARIOUS PHYSICAL PROPERTIES OF THE WATER MEDIUM

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ABSTRACT

High pH and oxygen but low total carbon dioxide values were recorded from water at sites containing high percentage covers of predominantly submerged aquatic vegetation. The converse was true in water at sites containing very dense covers of predominantly rooted-floating and free floating aquatic vegetation. The cover of submerged aquatic vegetation was shown to be influenced by the turbidity of the water and also by shading, particularly by that of floating aquatic vegetation.

UITTREKSEL

SOMMIGE ONDERLINGE VERWANTSKAPPE WAARGENEEM TUSSEN DIE WATERPLANT-BEDEKKING EN VERSKEIE FISIESE EIENSKAPPE VAN DIE WATERMEDIUM

Hoë pH en suurstof – maar lae koolsuurgas waardes kom voor in water uit standplase met 'n hoë persentasie bedekking van hoofsaaklik onderwaterse hidrofiete. Die teenoorgestelde het egter geblyk in water uit standplase met 'n digte bedekking van hoofsaaklik geworteld-drywende en drywende plantegroei. Die bedekking van onderwaterse hidrofiete word deur die turbiditeit drywende plantegroei.

INTRODUCTION

The following observations represent additional field data collected during the course of a detailed ecological survey conducted on the aquatic plants in the Pongolo River flood plain pans (Musil, Grunow & Bornman, 1973). These pans are situated along the Pongolo River in the North-east section of Tongaland between the Strijdom Dam at Jozini and the confluence of the Pongolo and Usutu Rivers in the Co-ordinates 27°S 32°E (quater degree square A). For the purposes of this study the aquatic plants include all the macroscopic plants, found growing in water.

MATERIAL AND METHODS

At various points on selected pans in the Pongolo River flood plains, sample sites were located after subjectively assessing the overall species composition and habitat conditions. It was regarded as most important that each of these

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Accepted for publication 16th October, 1975.

sites be as uniform as possible. Each sampling site was subdivided into stands (stand samples) which followed contours representing various depths; the contour lines were more or less parallel to the shore (Fig. 1).

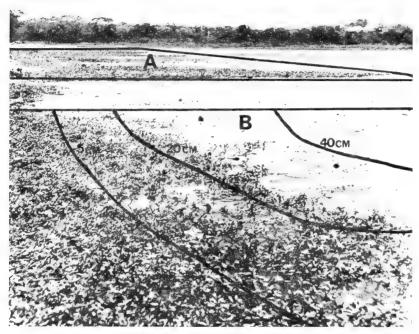


Fig. 1.

View southward of eastern shores of Omengu Pan with two sample sites A and B. Sample site B is subdivided into stands of 5, 20 and 40 cm water depths.

Frequencies, covers, and importance values of species were obtained in the following manner:

(1) Species frequency was calculated from data obtained from forty 0,25 m² quadrats thrown in a stratified random fashion in each stand. Curves (Fig. 2) were constructed from data obtained from three different stands (a) containing a dense cover, (b) an intermediate cover and (c) a low cover of aquatic vegetation, to determine whether this number of quadrats was a satisfactory sample size. Thirty quadrats per stand was found to be the minimum satisfactory sample size.

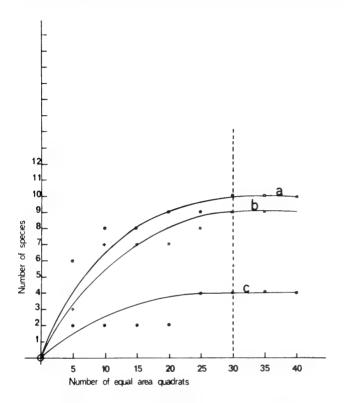


Fig. 2. Species-area relationships from three different localities.

(2) Species cover was calculated from point quadrats thrown in a stratified random fashion in each stand. Point quadrats were thrown until 80 strikes on the dominant plant species present were obtained. This ensured that the information content in each stand was kept constant. Standard errors of the means calculated on point quadrat data, sampled in various test stands with intermediate covers, prior to the investigation indicated that the above-mentioned number of strikes would ensure that the ensuing data had a standard error of less than 10 per cent of the mean. A Chisquare test for homogeneity, that is, uniformity of distribution of the plant species present was also conducted on point quadrat data obtained in each

stand. For the same reason and in the same way as Curtis and McIntoch (1951), only the strikes contributed by species with a relative percentage cover of 25 and above were tested for homogeneity at the 5 per cent level of significance. Point quadrat data taken sequentially were divided into four groups for the purpose of the test. The Chi-square test, therefore, had three degrees of freedom corresponding to a tabular value of 7,815. If a calculated value for the observed data was equal to or smaller than this, it was taken to indicate homogeneity.

(3) Importance values of species in each stand were calculated according to the formula: IV = 2 Relative % Cover + Relative % Frequency/3. Species density was not included in the formula as individuals could not be distinguished in some species of aquatic plants, particularly those exhibiting a stoloniferous habit, e.g. Ludwigia stolonifera (Guill. and Perr.) Raven., Echinochloa pyramidalis (Lam.) Hitchcock and Chase., Ipomoea aquatica Forsk. The relative percentage covers were regarded more significant and were, therefore, weighted appropriately.

Water

Water samples and readings were taken at midday as far as possible on clear calm days. The pH of the water in each stand was measured with a portable

TABLE 1 Effect of vegetation type on pH of surrounding water.

Pan	Date	Vegetation	Some principal species	Depth of Water cm	Average pH
Nhlole Nhlole	September September	rooted/floating rooted submerged	Nymphaea lotus Najas pectinata Potamogeton crispus	40 60	7,5 8,2
Msinyeni Msinyeni	May May	rooted submerged rooted/floating	Potamogeton crispus Nymphaea lotus	40 40	7,5 7,2
Sokunte Sokunte Sokunte	October October October	rooted submerged rooted submerged	Echinochloa pyramidalis Ludwigia stolonifera Najas pectinata Najas pectinata	5 40 100	7,7 8,2 8,1
Mandlankunzi Mandlankunzi	June June	rooted submerged rooted/floating	Potamogeton crispus Ludwigia stolonifera Pistia stratiotes Scirpus cubensis	50 50	7,7 7,1
Mandlankunzi Mandlankunzi	September September	rooted submerged rooted/floating	Potamogeton crispus Ludwigia stolonifera Pistia stratiotes Scirpus cubensis	50 50	8,9 7,1

meter while O_2 concentrations were measured using a galvanic-cell oxygen analyser with a lead-silver electrolyte probe. The total CO_2 (HCO $_3$ + CO $_3$) was calculated from the total alkalinity which was estimated according to the method of Golterman (1969). Generally ten readings of pH and O_2 concentrations were taken at each sampling while four water samples were taken for determination of total alkalinity. The above number of readings were sufficient to give a standard error of less than one per cent of the mean for pH and O_2 concentrations and five per cent of the mean for total CO_2 (HCO $_3$ + CO_3).

A secchi disc was used to determine the turbidity of the water in each of the stands. In most cases secchi disc readings were determined over a number of days to obtain the best average figure for a particular stand.

RESULTS

An initial comparison between the average pH values recorded in some stands and the type of aquatic vegetation present, whether rooted and free floating

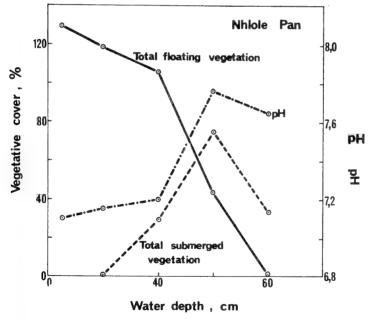


Fig. 3. Effect of vegetation type and its cover on pH of surrounding water.

or submerged, are represented in Table 1. Neutral or more acidic values were found in stands containing predominantly free floating and rooted-floating vegetation and alkaline values in stands with predominantly submerged aquatic vegetation.

The possibility that each vegetation type modified the pH of the surrounding water was illustrated in Nhlole Pan. When the total percentage covers of (a) the rooted and free floating aquatic vegetation and (b) the submerged aquatic vegetation, as measured in a series of stands of increasing depth, were plotted against the average pH values recorded in each of these stands at two separate dates (Fig. 3), it was found that as the pH values rose, the total percentage cover of the free floating and rooted-floating aquatic plants decreased while those of the submerged aquatics increased with increasing depth. As the percentage cover of the submerged aquatics declined from the 60 to the 80 cm depth, so did the pH values. This indicated that it was possibly the actual quantity of each vegetation type present that determined the pH of the water immediately sur-

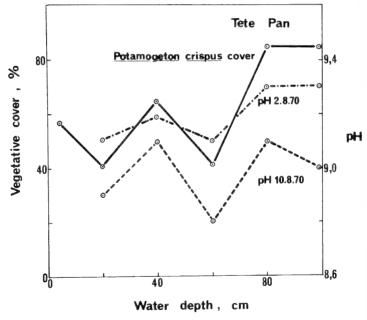


Fig. 4. pH of water as influenced by the cover of submerged aquatic vegetation.

rounding it. The greater the percentage cover of submerged aquatic vegetation recorded the more alkaline the pH was.

This phenomenon was clearly illustrated in a comparison between the percentage cover of *Potamogeton crispus* and the average pH values, measured on two different dates in a series of stands of increasing depth at one sample site on Tete Pan. Figure 4 shows that all the pH values were high, as expected, since the only species present was *Potamogeton crispus*, a submerged rooted aquatic. The more alkaline the pH value the higher the actual percentage cover recorded for *Potamogeton crispus* in each stand. In fact, curves for pH and percentage cover of this species complemented one another.

Like pH, the differences measured in the total CO₂ and O₂ content of pan water at various localities were also attributed to the quantity of each vegetation type found in the immediate vicinity. Table 2 shows that higher pH and O₂ values and lower total CO₂ values were recorded from water in stands containing high percentage covers of predominantly submerged aquatic vegetation (Tete). On the other hand, low pH and O₂ values but high total CO₂ values were recorded in stands containing extremely high percentage covers of predominantly rooted-floating and free floating vegetation (Mniati, Mandlankunzi).

The low total O_2 values but high pH values were attributed to the removal, by submerged aquatic vegetation, of CO_2 from the water during photosynthesis, resulting in a decrease in the total carbonic acid content present in solution, this initiating a rise in pH. The high O_2 values recorded from these stands were considered due to the O_2 released into the water by the submerged aquatic vegetation during photosynthesis. The high total CO_2 and low O_2 content of

TABLE 2
A comparison between pH, total CO₂ (as HCO₃+CO₃) and O₂ values recorded in stands with different total percentage covers.

Pan	Site	Depth of water cm	Total % cover floating vegetation	Total % cover submerged vegetation	Average pH	Average CO ₂ (as HCO ₃ + CO ₃) mg/1	Average O ₂ mg/1
Tete Tete	E E	80 100	=	85,0 85,0	9,2 9,1	29,9 23,3	9,7 9,6
Nhlole Omengu	DCA NEA	20 80	119,6 110,6	8,0	7,1 7,4	69,8 62,4	6,0 5,1
Mniati Mandlankunzi Mandlankunzi	M MI MI	80 80 60	180,0 258,2 248,9	13,1 5,7	6,4 6,3 6,3	213,9 117,9 117,9	2,0 1,9 1,9
Banzi Banzi	SW NE	Sub —	ojective visua 100,0 40,0	al assessment 0,0 5,0	of cover. 6,3 7,1	_	3,4 8,0

water in stands was attributed to the active respiration of the fauna beneath the vegetation and to the submerged portions of the plants. The acidic pH values, on the other hand, were attributed to an increase in carbonic acid and possibly also to humic acids arising from decomposing plant litter of the floating vegetation. It was considered, too, that diffusion of O_2 from the atmosphere into the water and CO_2 from the water into the atmosphere was limited by the dense cover of floating vegetation.

In stands with somewhat intermediate covers of submerged and free floating and rooted-floating aquatic plants more or less intermediate pH, total CO_2 , and O_2 values were recorded (Nhlole, Omengu). It is possible that the ultimate values recorded in these stands depended on the combined reaction of each vegetation type with the surrounding water, the extent of which depended on the quantity of each vegetation type present.

The reaction of the submerged aquatic vegetation on the surrounding water was further emphasised in general seasonal studies conducted in Tete Pan. In

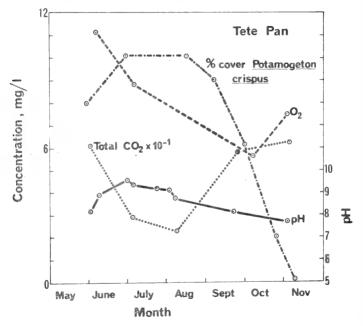


Fig. 5.
Seasonal changes in pH and total CO₂ concentration of water as influenced by changes in cover of *Potamogeton crispus*.

this pan a correlation was shown to exist between the pH and total CO₂ as measured monthly in representative water samples and the percentage of total water surface area covered by *Potamogeton crispus* as subjectively assessed monthly from June to November (Fig. 5). The curves show that a peak cover of *Potamogeton crispus* during the July/August period coincided with peak pH values and minimum total CO₂ values recorded in this pan during this period. As the cover of *Potamogeton crispus* decreased towards November the total CO₂ values rose with a concomitant drop in pH.

The effects of shading of rooted and free floating aquatic plants on the cover of submerged aquatic plants is illustrated in a graph plot of the sum total of importance values of submerged aquatic vegetation and those of rooted and free floating aquatic vegetation as measured in a series of stands of increasing depth at one sample site on Omengu Pan (Fig. 6). The graphs are virtually

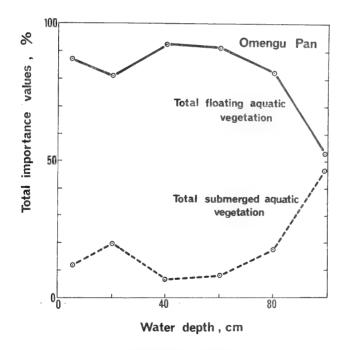


Fig 6.

The inverse relationship between floating and submerged aquatic vegetation in terms of total importance values.

inverted images of each other indicating an inverse correlation between the two types of aquatic vegetation. It is evident that the higher the importance values calculated for the rooted-floating and free floating vegetation, the larger the total relative percentage cover and frequency and consequently the more intense the shading effects on the submerged aquatic vegetation. This would possibly reduce photosynthesis in the submerged aquatic vegetation and consequently limit its growth.

The availability of light to the submerged aquatic plants was not only limited to the effect of shading by rooted-floating and free floating aquatic plants but also to the turbidity of the water. For example, at one particular sampling site on the leeward margin of Tete Pan, the percentage covers of *Potamogeton crispus*, the dominant submerged aquatic plant species present, were assessed in a series of stands of increasing depth. A series of secchi disc readings were also taken in these stands over a number of days. Figure 7 illustrates the results

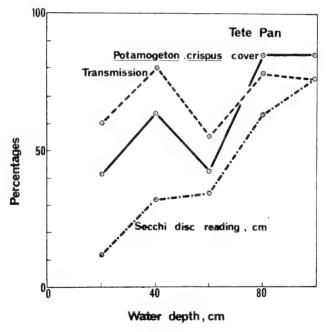


Fig. 7.

Relationship between percentage cover of *Potamogeton crispus* and turbidity of water plotted as percentage transmitted light.

graphically. The curves show that as the water depth increased so did the secchi disc readings, the water obviously becoming progressively less turbid. The smaller average secchi disc readings measured at 20, 40 and 60 cm depths were attributed to the disturbance of the bottom substrate by cattle being brought to water every day. In fact, as Table 3 shows secchi disc readings in these three stands in the early morning before the cattle came to water were much higher than those later in the day.

TABLE 3
Secchi disc readings at different depths in Tete Pan.

Water depth cm	Average secchi disc reading cm		
20 40 60 80 100	August early morning 19,0 33,0 35,5 66,0 76,5	August late afternoon 5,0 31,5 32,5 61,0	

Comparison between the average secchi disc readings and the percentage covers of *P. crispus* recorded in each stand (Figure 7) revealed that as the percentage cover of *P. crispus* increased from 20 to 40 cm depth so did the average secchi disc readings. At 60 cm depth, however, the average secchi disc readings remained more or less constant while the percentage cover of *P. crispus* decreased. As the secchi disc readings again increased at 80 and 100 cm, so did the percentage covers of *P. crispus*. From these observations it appeared that if the water depth remained constant and its turbidity increased, the percentage cover of *Potamogeton crispus* would decrease, while at a constant turbidity (or secchi disc reading) if the water depth increased the percentage cover of *Potamogeton crispus* would correspondingly decrease.

The relationship between the percentage cover of P. crispus and the turbidity of the water became very much clearer when the average secchi disc readings were standardised and plotted as percentage light transmitted at each depth. This was calculated according to the formula, Average secchi disc reading $cm \times 100/depth$ of water cm. Therefore, an average secchi disc reading of 12 cm at 20 cm water depth gave a value equivalent to 60 per cent transmission. When a plot of the per cent transmission was compared with that of the per cent cover of P. crispus, the curves appeared to be mutually complementary, that is, the greater the per cent transmission of light the larger the per cent cover of P otamogeton crispus.

In concluding it should also be pointed out that the depth at which *Potamogeton crispus* yielded an optimal percentage cover was generally equivalent

to the maximum secchi disc reading measured in a particular pan: For example, the maximum secchi disc reading measured in Tete Pan at the beginning of August was 78 cm while the optimum percentage cover of *P. crispus* corresponded to the 80 cm depth. In Msinyeni the maximum secchi disc reading measured in October was 10 cm while the optimum percentage cover of *P. crispus* was measured at 10 cm depth (Table 4).

TABLE 4
Relationship between the turbidity of water and percentage cover of *Potamogeton crispus*.

Water depth cm	Percentage cover from	from point quadrat data		
5 10 20 40 60 80 100	Tete Pan (August) 57 42 65 43 85 85 *Maximum secchi disc reading Te (August)=78 cm *Maximum secchi disc reading Maximum secchi disc reading secchi disc reading secchi disc reading secchi disc reading secchi disc readin			

CONCLUSIONS

The high pH and O_2 values and low total CO_2 values recorded from water containing high covers of predominantly submerged aquatic vegetation were attributed to a removal of CO_2 and release of O_2 into the water by the photosynthesising vegetation. Alternatively, the low pH and O_2 values but high total CO_2 values recorded from water containing extremely dense covers of predominantly rooted-floating and free floating aquatic vegetation were perhaps attributable to the active respiration of the fauna beneath the vegetation and to the submerged portions of the plants, as well as to humic and other organic acids arising from decomposing plant litter from the floating vegetation.

The cover of submerged aquatic vegetation was shown to be limited by the degree of light penetration into water which, in turn, was dependent on the degree of shading by the floating aquatic vegetation and the turbidity of the water. It was considered that the less light available to the submerged aquatic plants, the smaller their growth rate due presumably to a lower photosynthetic activity.

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BOOK REVIEWS

NATAL WILD FLOWERS, by Barbara Jeppe, with pp. $(220 \times 290 \text{ mm})$ xiii, 1-118+56 full page colour plates, one map and several pencil sketches. Cape Town: Purnell, 1975. R20,00.

For many years a popular book on the wild flowers of Natal has been unavailable to the interested public. This latest book by Barbara Jeppe, perhaps best known for her very popular book on the Aloes of South Africa, will certainly go a long way towards filling this gap. The book is, however, essentially one for popular consumption and for the Africana Book collector.

Ross, in his recent *Flora of Natal*, listed some 4 800 angiosperm species for the Province, the smallest Province in the Republic of South Africa. In the book under review only 266 species are reproduced in colour and 16 in pencil, giving a total of 284 species. However, the cross-section through the flora is fairly representative. The text is simply written in essentially lay language and contains interesting information on such aspects as propagation, distribution and habitat. Where known the plant's common name, or names, are given. The book is well indexed, with separate indices to common and scientific names, but there is no bibliography.

The book contains some misconceptions, such as a reference to the "tundra-like" vegetation of the high Drakensberg, when this vegetation is strictly Afro-montane. There are also the inevitable small errors such as the incorrect spelling of Ixopo and Kosi on the map (given as Ixoxo and Kasi respectively) and the lack of a letter i on plate 52 for Begonia geranioides. Some minor inaccuracies and omissions occur in the text, such as the height of Scabiosa columbaria is given as about 50 cms when one metre would have been more accurate, and it would have been useful to mention that the fruits of Clivia miniata are best left to drop off the inflorescence before being placed in leaf-mould where they may take up to nine months to germinate.

A point of criticism directed at the author is that it is a pity that the species order used does not follow a taxonomic system. Plate 25, particularly, contains a mixture of families: Campanulaceae, Caryophyllaceae, Commelinaceae, Dipsacaceae, Getianaceae and Plumbaginaceae. The major disappointment of the book, however, is the quality of the reproduction of the colour plates. The pencil sketches have been well reproduced, but such a coarse screen has been used for the colour plates that there has been loss of detail. Also, scant attention has been paid to the colour balance of some plates, particularly Plate 2, where the leaves of Zantedeschia aethiopica and Stylochiton natalense are far too blue. Finally the pale colours have not always reproduced well and there is considerable loss of detail in some plates such as Plate 29 (Acacia nigrescens) and Plate 7 (Galtonia candicans).

This book is not a field guide to the wild flowers of Natal, but merely a portfolio of a selected cross-section of species. As such it fills a long felt gap in the range of books available

on the flora of South Africa.

E. Moll

DICTIONARY OF CULTIVATED PLANTS and their centres of diversity; excluding ornamentals, forest trees and lower plants, by A. C. Zeven and P. M. Zhukovsky, with pp. 219, 91 maps. Cloth bound. Wageningen: Centre for Agricultural Publishing and Documentation (Pudoc), 1975. Price D.fl. 45.

This is a most extraordinary concoction and, perhaps, symptomatic of the current malaise

in plant science.

It started inauspiciously as a paper in a Russian botanical journal dealing specifically with centres of origin of cultivated plants and their (presumed) genetically related wild species. This was subsequently expanded in book form published in 1970. The present work is based upon this latter production but is again very much enlarged.

The stated aim is to give the reader quick reference to the Centre of diversity of a cultivated plant species and, in some cases, of related wild species. These are very important, both genetically for breeding purposes and in the establishment of nature reserves. In man's quest for new or improved plant foods with which to titillate - or sustain - the palates of the proliferating millions, such genes will be of inestimable value.

The fact that the world's reservoir of genetic diversity is being recklessly depleted in order to accommodate the millions - who will inevitably be conditioned to a nagging subsistence level of near-starvation - seems not to disturb the complacent and puffy features of our modern sociologists, economists and 'hired' scientists. On no account must one's attention be diverted from feeding the increase to the more realistic programme of preventing the increase.

The dictionary is introduced by a couple of sections on the origin of agriculture and plant domestication, cradles of agriculture and centres of diversity. The remainder is devoted to the 2 300 species listed according to botanical families in each of the major centres - Chinese -Japanese, Indochinese - Indonesian, Australian, Hindustani, Central Asian, Near Eastern, Mediterranean, African, European—Siberian, South American, Central American and Mexican, North American. Some species have no recognizable gene centre and are listed separately. There is a substantial bibliography and an index of botanical names. Chromosome numbers, vernacular names and common uses are included with each description. Good value, one might say, for the hectic price but in my estimation this is not wholly so.

The errors are positively alarming. The publishers blurb is even inaccurate. They give 224 pages of text and 109 maps: my review copy has 217 effective pages and only 91 maps. Forest trees are supposedly excluded; I found a number mentioned.

Taking the African Centre as an example. There are no less than thirty-six taxonomic errors to start with. Wageningen has a world-renowned taxonomic institute; I should have thought it would have been possible to ensure accuracy in this regard at least. Poor botanists! They labour incessantly to improve the lot of the worker in the field, as well as to standardize our nomenclature, and seemingly the specialists take not a jot of notice.

Citations of authors and the spelling of many are frankly awful. One's appetite is whetted by a citation in the text – Churcher and Smith 1972 for example – only to find that it is not

included in the references.

For a Pudoc production, substantially bound and elegant though it is, one is surely entitled to more reliable contents? Even our own 'Buchu' and 'Rooibos tee' plants are incompetently presented. I have merely indicated some of the errors in the African section but there are just as many in several of the others except, perhaps, the European-Siberian Centre!

For the cautious researcher, this could be a useful rhinestone pendant to the crown jewels of Purseglove's Tropical Crops: for the student or those with little practical experience

of the tropics it could be very, very misleading.

O. Kerfoot

EMBRYOLOGY OF JUBAEOPSIS CAFFRA BECC.: 2. MEGASPORANGIUM, MEGASPOROGENESIS AND MEGAGAMETOGENESIS

B. L. ROBERTSON

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ABSTRACT

The ovary of *J. caffra* contains three uniovulate locules. These ovules, which are without a funicle, are intermediate between orthotropous and hemitropous.

The ovule is crassinucellate and bitegmic with procambium strands in the outer integument only. The inner integument, which becomes tanniniferous, forms an operculum.

Megasporogenesis results in the formation of either a linear or T-shaped tetrad of megaspores. Megagametogenesis results in the formation of a Polygonum type embryo sac with persistent synergids and ephemeral antipodal cells. A postament is present in the mature embryo sac.

UITTREKSEL

EMBRIOLOGIE VAN *JUBAEOPSIS CAFFRA* BECC.: 2. MEGASPORANGIUM, MEGASPOROGENESE EN MEGAGAMETOGENESE

Die vrugbeginsel van *J. caffra* is drie-lokulêr met 'n enkele saadknop in elke hok. Hierdie saadknoppe besit geen funikulus nie en is intermediêr tussen ortotroop en hemitroop.

Die saadknop is krassinuselleer met twee integumente. Prokambium stringe kom slegs in die buite-integument voor. Die binne-integument, wat op 'n latere stadium tannienvormend word, vorm 'n operkulum.

Megasporogenese lei tot die vorming van of 'n lineêre of 'n T-vormige tetrade van megaspore. Megagametogenese lei tot die vorming van 'n Polygonumtipe embriosak met blywende sinergiede en efemere antipodale selle. 'n Postament is aanwesig in die volwasse embriosak

INTRODUCTION

Apart from a publication on the microsporogenesis and microgametogenesis of *J. caffra* (Robertson, 1976), no other data relating to embryological aspects of this unique species are available.

In the Palmae generally, there appears to be a wide variation with respect to ovule structure. Davies (1966) states that palm ovules are anatropous to hemi-anatropous and bitegmic while Moore and Uhl (1973) report that many are in fact tri-tegmic, i.e. with an aril.

Three types of megagametogenesis have been described for the Palmae. The Allium or bisporic type (Maheshwari, 1950) occurs in *Chamaedorea latifolia* (Jonsson 1879–80 cited by Davis, 1966), *Nipa fruticans* (Radermacher, 1925 cited

Accepted for publication 3rd October, 1975.

by Maheshwari, 1950) and *Hyphaena indica* (Mahabale & Chennaveeraiah, 1957).

The second type is reported by Quisumbing & Juliano (1927) for *Cocos nucifera*, viz. the tetrasporic, eight-nucleate or Adoxa type (Maheshwari, 1950). These authors admit however that their findings conflict with Bauch (1911, cited by Quisumbing & Juliano, 1927) who claims to have observed degenerating megaspores during the late stages of sporogenesis and one is consequently left in some doubt as to which of the above two reports is correct.

The majority of palms appear to follow the third developmental pattern, viz. the monosporic, eight-nucleate or Polygonum type (Maheshwari, 1950) of embryo sac development (Swamy, 1942; Venkato Rao, 1955a, b; 1956a, b; 1958; Davis, 1966).

The actual structure of the embryo sac is not constant in the Palmae. In most cases a postament or podium is absent while in other species, e.g. *Areca catechu* (Venkato Rao, 1958) it is present. So, too, there is a variation in the role played by the antipodals. In *Hyphaene indica* (Mahabale & Chennaveeraiah, 1957) the antipodal nuclei remain naked, in *Areca catechu* (Venkato Rao, 1958) they are persistent and aggressive while in most other studied species they are ephemeral (Davis, 1966).

MATERIAL AND METHODS

Initially female flowers were obtained from four entire inflorescences which were cut down at various stages of development. However, it soon became apparent that all the female flowers on a single inflorescence were more or less at the same stage of development. Consequently, in order to avoid the destruction of too many inflorescences, it was necessary to leave the inflorescence attached to the tree and simply split the woody covering bract longitudinally open and collect the fl wers at weekly intervals.

These were fixed in either Craf II or F.A.A. (Sass, 1958), dehydrated in an ethyl alcohol/tertiary butyl alcohol (TBA) series, embedded in paraffin wax (55°C) and ectioned at 10 μ m on a rotary microtome as prescribed by Brooks, Bradley and Anderson (1950). The sections were stained in safranin/fast green (Holtzhausen, 1972).

RESULTS AND DISCUSSION

Megasporangium

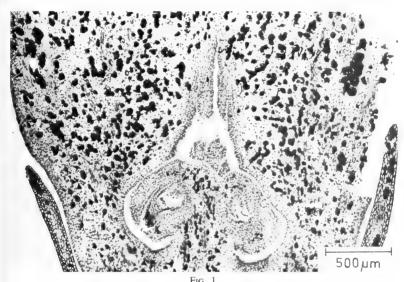
The ovary of *J. caffra* is comprised of three carpels whose loculi extend upwards in the form of a 3-radiate canal (Fig. 1) to join the stylar canal.

Placentation of the ovules is free-central (Fig. 1). The ovule is without a funicle and arises directly from the placenta (Figs 1, 2). Ovules of the genus *Bactris* are also without funicles (Venkato Rao, 1958).

In a longitudinal section through the ovary, the ovule is curved downwards by

approximately 45° (Figs 1, 2, 5A) and consequently it is neither truly orthotropous nor fully hemitropous. This is in contrast to the general condition found in the Palmae as a whole where the ovule is basically anatropous (Eames, 1961).

The ovule is bitegmic and the two integuments are fused together up to a point approximately midway between the chalaza and the micropylar end of the nucellus (Fig. 2). Initially the outer integument does not enclose the inner one (Fig. 3) suggesting that differentiation of the inner integument is initiated before that of the outer. By the time that the megaspore mother cell has differentiated though, the outer integument fully envelops the inner one as well as the nucellus and both

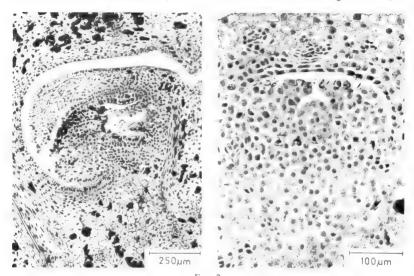


Longitudinal section through a female flower of *J. caffra* showing the freecentral placentation of the ovules.

integuments form the micropyle. The exostome and endostome are in line with each other and consequently the micropyle is straight, and points slightly downwards (Fig. 5A).

The outer integument is between five and seven cell layers thick and dominates the ovule by its massive structure. During megasporogenesis and the early stages of megagametogenesis the cells of the outer integument are fairly homogeneous, but by the time the embryo sac reaches maturity, the epidermis cells of the distal portion of this integument become anticlinally elongated (Fig. 2). At this stage too, the cells constituting the central tissues of the outer integument become disorganized.

The inner integument is a much more delicate structure and along the sides of the nucellus it is usually only two cell layers thick. Occasionally it may be three cell layers thick at this point (Fig. 6C). At the micropyle, the inner integument widens to form an operculum (Figs 6B, C). The cells of the operculum start to accumulate tannin from a relatively early stage and by the time the embryo sac reaches maturity, many of the operculum cells are tanniniferous (Figs 6B–F, 7).



Longitudinal section through the ovule during the late stages of megagametogenesis. No funicle is present.

Fig. 3.

Transverse section through a portion of the ovary showing a young ovule, longitudinally sectioned, during differentiation of the integuments.

During megasporogenesis the cells of the inner integument undergo differentiation. The cells of the inner epidermis of this integument, i.e. the integumentary cells lying directly adjacent to the nucellus elongate radially to form an integumentary tapetum or endothelium (Figs 5C, 6A–D). They remain uninucleate and divide anticlinally to keep pace with the increasing volume of the developing embryo sac.

In *J. caffra* the nucellus at the chalazal end of the embryo sac remains intact until after fertilization, but the nucellar tissue in the micropylar half of the ovule degenerates from a relatively early stage during megagametogenesis (Figs 6C, D) and contrary to the general statement made by McLean & Ivimey-Cook (1964) it

is felt that although the endothelium might well be involved in the nutrition of the embryo sac, the protective and restraining function of this layer of cells must not be overlooked.

With regard to the nucellus of the ovule, two terms are in general current use, viz. crassinucellate and tenuinucellate. Unfortunately these two terms have been rather loosely used (Davis, 1966) and various authors have defined them differently. Maheshwari (1950) and Davis (1966) use the presence or absence of one or more parietal cell layers between the megaspore mother cell and the nucellus epidermis as the criterion for distinguishing between crassinucellate and tenuinucellate ovules. Eames (1961) also makes use of the parietal tissue in his definitions, but considers the actual structure of the nucellus as a whole, i.e. whether it is massive, or small and delicate, as a more important criterion. McLean & Ivimey-Cook (1964) on the other hand disregard the parietal tissue entirely and use only the size (massive or delicate) and the longevity (relatively persistent or ephemeral) to differentiate between the two types.

The hypodermal archesporial cell of *J. caffra* (Fig. 4) divides periclinally to form a single parietal layer and the megaspore mother cell (Fig. 5A). Thus according to the definitions of Maheshwari (1950) and Davis (1966) the ovule of *J. caffra* is crassinucellate. Figs 5A, 5C, 6B however, show that the nucellus is by no means massive but rather, in the words of Eames (1961) "small and delicate". The nucellus is also not very persistent (except for the postament) but rather ephemeral. Consequently the ovule could be considered tenuinucellate if one was to employ the definitions of either Eames (1961) or McLean & Ivimey-Cook (1964).

The definitions of Maheshwari (1950) and Davis (1966) are perhaps more standard than those of Eames (1961) and McLean & Ivimey-Cook (1964) and consequently the ovule of *J. caffra* will be classified as crassinucellate.

It is felt that the term crassinucellate in general is too wide and that a more specific terminology should be devised for more precise descriptions of this type of nucellus. Maheshwari (1950), for example, describes two types of tenuinucellate ovules, depending on the position of the point of origin of the integuments.

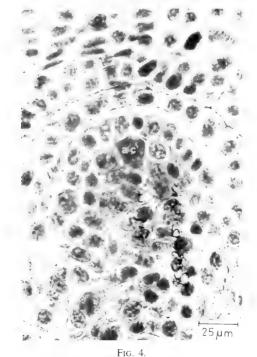
The nucellus closest to the micropyle starts to degenerate at an early stage in the development of the female gametophyte (Figs 6C, D) and by the time the embryo sac reaches maturity only a single, disorganized layer of nucellus cells lies between the embryo sac and integument (Fig. 7). The nucellus at the chalaza however is persistent and in a longitudinal section through the ovule it can be observed as two "horns" stretching from the chalaza down towards the micropyle (Fig. 7). A similar nucellar structure, i.e. a postament occurs in a number of other palm species, e.g. Caryota mitis, Chrysalidocarpus lutescens, Actinophloeus macarthurii, Howea belmoreana, Areca triandra and A. concinna (Venkato Rao, 1958). The postament does not persist very long after fertilization and cannot be observed after embryo development has started.

Vascular tissue from the placenta to the ovule mostly terminates in the chalazal region. A small amount of vascular tissue continues into the outer integument, but it is relatively poorly differentiated and occurs mainly in the form of procambium strands.

Archesporium

Very early in the ontogeny of the ovule, before the primordia of the integuments are visible, a single hypodermal cell in the apex of the nucellus becomes conspicuously larger with denser cytoplasm than the surrounding nucellus cells (Fig. 4). This cell constitutes the archesporium of *J. caffra*.

As development of the ovule progresses, the archesporial cell divides periclinally to produce the primary parietal cell and the primary sporogenous cell. No further periclinal divisions occur in the former cell. It does however divide anticlinally to keep pace with the increase in volume of the nucellus. The single megaspore mother cell, which normally differentiates directly from the primary



Longitudinal section through nucellus primordium in which the archesporial cell (ac) has differentiated. No integumentary development has as yet been initiated.

sporogenous cell without any intervening divisions, is thus separated from the nucellus epidermis by a single cell layer of parietal tissue.

Abnormal ovules occasionally occur in which more than one megaspore mother cell are present.

The archesporial development of J. caffra thus conforms to Type III as described by Schnarf (cited by McLean & Ivimey-Cook, 1964) for angiosperms generally.

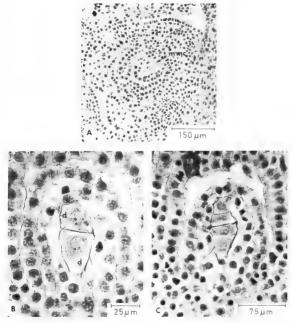


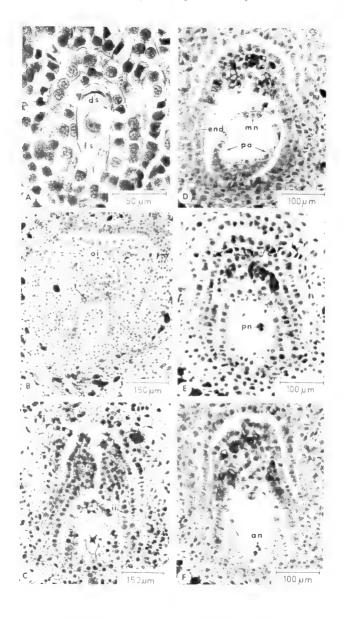
Fig. 5.

Megasporogenesis in *J. caffra*. A – Megaspore mother cell (mmc). B – Megaspore dyad cells (d). C – Linear tetrad of megaspores.

Megasporogenesis

The mature megaspore mother cell is relatively large and typically it is elongated parallel to the long axis of the nucellus (Fig. 5A). This mother cell contains a large nucleus with a conspicuous nucleolus.

Megasporogenesis is successive, i.e. cell walls are laid down after each of the two division during meiosis. The megaspore mother cell undergoes meiosis and as always, the first division is transverse to the long axis of the nucellus to form two dyad cells (Fig. 5B). Each of these two cells divides again to form the megaspore



tetrad. In all cases the chalazal dyad cell divides transversely. The micropylar dyad cell can however divide either transversely to form a linear tetrad (Fig. 5C) or longitudinally to form a T-shaped tetrad. The T-shaped tetrad appears to be more common than the linear one. In the T-shaped tetrad, the division of the micropylar dyad cell occurs in such a plane that only three megaspores are visible in a single transverse section through the ovary while the fourth megaspore lies either directly above or below the micropylar spore (still in transverse section).

The chalazal cell of the tetrad always functions and gives rise to the embryo sac while the three micropylar megaspores degenerate and become crushed by the expanding embryo sac (Fig. 6A).

Megagametogenesis

The development of the female gametophyte is initiated by the enlargement of the chalazal megaspore only (Fig. 6A), and the female gametophyte is therefore monosporic.

Enlargement of the functional megaspore is followed by three mitotic divisions, resulting in the formation of a 2-, 4- and eventually 8-nucleate embryo sac (Figs 6B–F).

Of these eight nuclei, three remain in the micropylar region of the embryo sac to form the egg apparatus (Fig. 6D); one nucleus from each pole migrates to the centre of the embryo sac where they fuse to form the secondary nucleus (Fig. 6E) and three remain in the chalazal end to form the antipodals (Fig. 6F).

Based on the structure of the mature embryo sac, the female gametophyte of J. caffra thus conforms to the Polygonum type (Maheshwari, 1950).

The two synergids are definite cells each with a large nucleus and nucleolus, very dense and dark staining cytoplasm and a series of small vacuoles arranged along the periphery of each cell, especially along the cell wall furthest from the micropyle, i.e. towards the inside of the embryo sac (Fig. 7). No hooks are formed and the synergids are attached to the embryo sac wall by a broad base. The free sides of these two cells are slightly rounded. No filiform apparatus is visible.

One of the synergids disappears just prior to fertilization while the other starts to degenerate shortly after fertilization. Its remains can however be observed until the pro-embryo is approximately eight- to sixteen-celled.

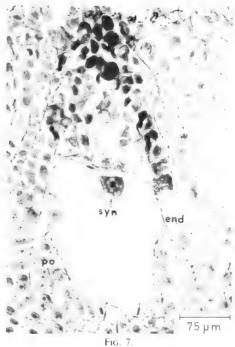
Fig. 6.

Megagametogenesis of *J. caffra*. A – Functional chalazal megaspore plus degenerating spores. B – Two-nucleate embryo sac. C – Four-nucleate stage of female gametophyte. Only three nuclei are visible in this figure. Note the operculum of the inner integument. D – Three micropylar nuclei which will form the egg apparatus. E – Fusion of the two polar nuclei during formation of the secondary nucleus. F – Three antipodal nuclei. Also visible are two micropylar nuclei.

⁽an—antipodals; ds—degenerating spores; end—endothelium; fs—functional megaspore; ii—inner integument; mn—micropylar nuclei; oi—outer integument; op—operculum; pn—polar nuclei; po—nucellar postament; t—tanniniferous cells).

The egg cell is somewhat smaller than the synergids and is situated slightly laterally to them with the result that all three cells of the egg apparatus can very rarely be observed in a single longitudinal section.

Three antipodal cells are present (Fig. 6F). These cells are small and relatively ephemeral, disappearing shortly after the formation of the secondary nucleus. By the time that the synergids are fully differentiated (Fig. 7) no trace of the antipodals is left.



A fully differentiated synergid. (end—endothelium; po—podium; syn—synergid).

Initially, i.e. up to the 2-nucleate stage, the embryo sac is a long narrow structure (Figs 6A, B). From this stage on however, the embryo sac enlarges very rapidly in both a longitudinal and transverse direction with the result that the nucellus, particularly in the vicinity of the micropyle, degenerates. The mature embryo sac is approximately 170 μ m long and 120 μ m wide.

Conclusions

In general the megasporogenesis and megagametogenesis of J. caffra is in accordance with that of the Cocoid palms studies by Venkato Rao (1958), viz.

Bactris major and Arecastrum romanzoffianum and a Polygonum-type embryo sac develops from the functional chalazal megaspore of the megaspore tetrad.

It is strange though that the embryology of *Cocos nucifera* and *J. caffra* should be so vastly different. These two species are very similar in many aspects, yet Quisumbing & Juliano (1927) report that a bisporic, Allium type of female gametophyte is found in *Cocos*. They differ further in that the archesporial cell of *J. caffra*, which becomes visible prior to differentiation of the integuments, divides to give rise to a parietal cell and a sporogenous cell, the latter of which differentiates into the megaspore mother cell; while in *Cocos*, the archesporial cell differentiates directly into the megaspore mother cell, or as Quisumbing & Juliano put it "... becomes the megaspore mother cell". Furthermore this cell (in *Cocos*) is not visible until both the integuments are fully differentiated (Quisumbing & Juliano, 1927).

ACKNOWLEDGEMENTS

This study was supported by research grants from the University of Port Elizabeth and C.S.I.R.

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A REVISION OF DIASTELLA (PROTEACEAE)

J. P. ROURKE

(Compton Herbarium, Kirstenbosch)

ABSTRACT

A revision of *Diastella* has been undertaken; 7 species are recognized. A key to the species is provided and distribution maps for each species are given. *Diastella* is upheld as a distinct genus, separated from *Leucospermum* on sound morphological characters. It is postulated that *Diastella* could have evolved from some of the small flowered species of *Leucospermum* such as are placed in *Leucospermum* Sect. *Diastelloidea*.

UITTREKSEL

'N HERSIENING VAN DIASTELLA (PROTEACEAE)

Die geslag Diastella is hersien en 7 soorte erken. 'n Sleutel tot die soorte en verspreidingskaarte vir elke soort word aangebied. Die duidelike onderskeidende morfologiese kenmerke van Diastella skei dit van Leucospermum. Daar word gepostuleer dat Diastella uit die Leucospermum soorte met klein blommetjies soos die in Leucospermum Seksie Diastelloidea kon ontwikkel het.

Introduction

Diastella, comprising 7 species, is a genus of small, almost herbaceous shrubs, endemic to the south-western Cape. By the close of the 18th century, most of the known species had been described, usually under the generic names of Protea or Leucadendron. Later, in 1809, R. A. Salisbury, writing in Joseph Knight's On the cultivation of the plants belonging to the natural order Proteēae, founded Diastella. while at the same time publishing a remarkably accurate revision of the genus. Brown (1810), however, did not recognize Diastella as construed by Salisbury. Instead, he expanded the concept of *Mimetes* Salisb. and divided it into 2 sections with the species placed by Salisbury in Diastella, being accommodated in Mimetes Salisb. sec. II Mimetes spuriae R.Br. This unnatural and awkward arrangement gave rise to untold confusion on the part of subsequent authors who ignored Salisbury (1809) but struggled desperately to justify the association of two very different morphological lines under one generic name. A detailed investigation of the problem by Phillips (1911) led to the reinstatement of Diastella Salisb. and the publication of a complete revision of the genus in 1912. The present revision has been undertaken in order that it might be used in the account of the Proteaceae being prepared for the Flora of Southern Africa.

GENERIC DEFINITION

Although members of the genus *Diastella* have a distinctive overall appearance, a clear, unambiguous definition is difficult to make, largely on account of the inclusion of *D. myrtifolia and D. parilis*. The majority of the *Diastella* species are easily characterized as they lack hypogynous scales, they have only terminal inflorescences (capitula), entire leaves, equal perianth segments, and the perianth tube is either absent or so short as to be barely perceptible. *D. myrtifolia* and *D. parilis* differ in that both these species have hypogynous scales, occasionally dentate leaves, inflorescences which are produced in both terminal and axillary positions, subequal perianth segments with the abaxial perianth segment being larger and longer than the 3 adaxial perianth segments and a perianth tube up to 2 mm long. These characters suggest an affinity with *Leucospermum* although the overall appearance of both *D. myrtifolia* and *D. parilis* is clearly similar to that of the other species of *Diastella*.

However, there is one morphological feature common to all species of *Diastella* as defined here: the *floral bracts are linear to filiform, hyaline and uniformly pubescent*. In addition, the involucre surrounding the inflorescence is usually 1–3 seriate and is composed of loosely arranged bracts, foliaceous to papyraceous in texture (often almost hyaline) and which exceed or equal the length of the perianth. A combination of the characters mentioned in this paragraph is considered to be the most reliable circumscription of *Diastella*.

In conclusion, it is perhaps worth noting that, after undertaking palynological studies on the genus, Erdtman (1966: 344) concluded that "Pollen morphology supports generical rank of *Diastella*".

EVOLUTIONARY SPECULATIONS

Variation patterns in two species, *D. divaricata* and *D. thymelaeoides* point to the continuing divergence of morphologically distinguishable geographical races (Figs. 5 and 7). Such patterns suggest that active speciation is still taking place in *Diastella*.

The case of *D. divaricata* is of particular interest since it may be used in an attempt to gauge the rate of speciation within the genus. Distribution and variation patterns are here interpreted in relation to recent palaeogeographic research (Dingle and Rogers, 1972a; Dingle and Rogers, 1972b).

Lower sea-levels during the Pleistocene would have resulted in the exposure of much of the Agulhas Bank and adjacent coastal areas. According to Dingle and Rogers (1972a), this lowering of the sea-level would have varied from -50 m at $11\ 000-9\ 000$ years before present, to -140 m at $20\ 000$ years before present. A regression of this magnitude would have permitted the ancestral stock of a species like D. divaricata to be continuously dispersed over an area extending from the Cape Peninsula to the Hottentots Holland Mountains, during the period $11\ 000$ to $20\ 000$ years before present. The marine transgression which followed after about

10 000 years before present, would have resulted in the flooding of False Bay and the accumulation of the unconsolidated dunes of the Cape Flats. It would also have effectively isolated two segments of the ancestral population of *D. divaricata*. Under conditions of isolation one may postulate that these two populations diverged and differentiated into two very distinct geographical subspecies (Fig. 5), and that this differentiation took place during the past 10 000 years.

RELATIONSHIP WITH OTHER GENERA

In a diagram indicating what they consider to be the most likely phylogenetic relationships in the Proteaceae, Johnson and Briggs (1975) show *Leucospermum* and *Diastella* on separate but almost parallel lines. However, it seems that *Leucospermum* and *Diastella* are even more closely related, as evidenced not only by their morphology but also by the occurrence of a natural, putative, bigeneric hybrid between them. (See Hybrids.)

As mentioned previously, two intermediate species, *D. myrtifolia* and *D. parilis* appear to link *Leucospermum* and *Diastella*. It is possible to derive *Diastella* from a hypothetical ancestor, which is most likely to have been a *Leucospermum* of the section *Diastelloidea*, by postulating a reduction series with *D. myrtifolia* and *D. parilis* occupying a transitional position. In such a hypothetical scheme, it is probable that the following changes have taken place in the development of *Diastella* from *Leucospermum*:

- (1) A change from axillary to terminal capitula.
- (2) A decrease in perianth size.
- (3) A reduction in the asymmetry of the perianth to the stage where the 4 perianth segments are free and equally developed.
- (4) The progressive reduction in the perianth tube until the 4 perianth segments are free to the base.
- (5) A reduction in the number of teeth at the leaf apex to the stage where entire leaves predominate.
- (6) A reduction in the woodiness of the plant from a fairly woody shrub with a clearly defined flowering period in *Leucospermum* to a very much less woody almost herbaceous shrublet in *Diastella* in which flowering takes place almost continuously throughout the year.

Finally, a consideration of the distribution pattern of *Diastella* shows that the genus is restricted to a rather small part of the south-western Cape – very different from the wide range of *Leucospermum*. With the exception of the monotypic *Orothamnus*, *Diastella* has the smallest distribution range of all the genera of African Proteaceae. (Fig. 1.)

Bearing in mind the foregoing remarks on the morphological affinities of *Diastella* with *Leucospermum* and also its restricted distribution range, the author considers it plausible to suggest that *Diastella* may well have evolved relatively recently (by comparison with related Proteaceous genera) and that the most likely

ancestral stock from which it could have been derived is *Leucospermum* sect. *Diastelloidea*.

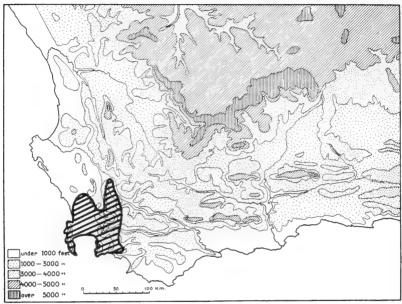


Fig. 1. Distribution of the genus *Diastella* Salisb.

A REVISION OF DIASTELLA

Diastella Salisb. in Knight, Cult. Prot.: 61 (1809); Phill. in J. Bot. Lond. **49:** 28 (1911); Phill. & Hutch. in Fl. Cap. **5:** 650 (1912); Hutch., Gen. of Fl. Pl. **2:** 289 (1967).

Mimetes Salisb. sect. II Mimetes spuriae R. Br. in Trans. Linn. Soc. Lond. 10: 109 (1810).

Mimetes Salisb. sect. Pseudomimetes Endl., Gen. Pl. Suppl. 4 (2): 78 (1848); Meisn. in DC., Prodr. 14: 264 (1856).

Lectotype: D. thymelaeoides (Berg.) Rourke – syn. D. bryiflora Salisb. ex Knight. (See Hutch., Gen. of Fl. Pl. 2: 289 (1967).

DERIVATION OF NAME

From the Greek, diastellein, to put asunder, separate or expand. The name apparently alludes to the deeply divided perianth segments which are free to the base or almost free to the base, resulting in a very short, almost imperceptible perianth tube, or no perianth tube at all

Small shrubs, erect, sprawling or decumbent; with slender stems. Leaves subimbricate to imbricate, oblong, orbicular, lanceolate-elliptic or acicular-terete, usually entire, occasionally with 2 or 3 apical teeth, puberulous to glabrous. Inflorescences globose, globuliform or broadly campanulate, 1-2 cm in diam. sessile; usually solitary and terminal, occasionally axillary and clustered. Involucral bractis 1-3 seriate, equalling or exceeding the length of the perianth; ovate, lanceolate, acute to acuminate, foliaceous to papyraceous in texture, often hyaline. Involucial receptacle flat to slightly convex, 1–2 mm in diam. Floral bracts linear to filiform, hyaline, uniformly pubescent on abaxial surface. Perianth 6-10 mm long, straight in bud, regular except in 2 species in which the abaxial perianth segment is slightly longer than the remaining three; limbs filiform to lanceolatelinear, acute to acuminate, glabrous or sericeous; claws filiform, sericeous, tube absent, scarcely perceptible or rarely up to 2 mm long. Anthers linear, acute, inserted at base of perianth limb. Style terete, filiform, 8-12 mm long; glabrous or pubescent proximally; curved before anthesis. elongating straightening later. Pollen presenter cylindric, filiform, scarcely differentiated from the style. Ovary ovoid 1 mm long, pubescent, with a solitary ovule. Hypogynous scales usually absent, present only in 2 species. Fruit an ovoid to cylindric achene, emarginate at base, glabrous to puberulous, greyish-white.

DIAGNOSTIC CHARACTERS

Diastella may be distinguished by having small globose to globuliform, terminal (rarely axillary) capitula, 1–2 cm in diam. with the perianth 6–10 mm long, with a 1–3 seriate involucre of somewhat loosely arranged foliaceous to papyraceous often hyaline bracts, equalling or exceeding the length of the perianth and with linear to filiform floral bracts, uniformly sericeous.

DISTRIBUTION

Seven species, endemic to the extreme south-western corner of the south-western Cape Province.

KEY TO THE SPECIES OF DIASTELLA

Hypogynous scales present Involucral bracts broadly ovate, prominent, drying brown and papyraceous
Involucral bracts oblong-elliptic, green and foliaceous, not very prominent
Hypogynous scales absent (2) myrtifolia
Leaves acicular
Outer surface of involucral bracts covered with a soft sericeous indumentum; stems of the current year's growth pubescent, leaves 5–15 mm long
Outer surface of outer whorl of involucral bracts glabrous (margins ciliate);

Leaves orbicular, oval, elliptic or lanceolate	
Perianth pink	
Perianth creamy-white	
Leaves 1–4 mm wide(4) fraterna	
Leaves 4–9 mm wide(5) thymelaeoides	

(1) **Diastella parilis** Salisb. ex Knight, Cult. Prot.: 62 (1809); Phill. & Hutch. in Fl. Cap. **5:** 653 (1912). Type: "By the river, Roode Zand Cascade", *Niven 44* (K!)

Mimetes myrtifolia R.Br. vars a & b R.Br. in Trans. Linn. Soc. Lond. 10: 110 (1810); Roem. & Schultes, Syst. Veg. 3: 385 (1818); Meisn. in DC., Prodr. 14: 265 (1856). Types: (of vars. a & b): Africa australis, Prom. bon spei, without collectors (BM!)

A low, erect, rounded shrub, 50–70 cm in height, with a single main stem. Stems pubescent, 1–2 mm in diam. Leaves oblong – elliptic 1–3 cm long, 2–5 mm wide, slightly twisted at base, apex acute and entire or obtuse to truncate with 2–3 apical teeth; softly velutinous. Inflorescences sessile 1,5–2 cm in diam., depressed globose, solitary and terminal or axillary with 2–6 inflorescences clustered towards the apex of a flowering shoot. Involucre prominent, 3 seriate. Involucral bracts broadly to very broadly ovate, 7–8 mm long, 4–5 mm wide, apices acute or blunt with a point; brown and papyraceous on drying, outer surface glabrous, margins ciliate. Involucral receptacle flat, 3 mm in diam. Floral bracts linear – filiform, densely sericeous. Perianth pink, 8–10 mm long, densely sericeous; tube 2 mm long, glabrous proximally, becoming sericeous distally; the abaxial perianth segment slightly longer than the remaining 3; limbs lanceolate – acute, glabrous at base but crinite at apex, abaxial limb sericeous and larger than the remaining 3. Style 10 mm long, straight, glabrous. Pollen presenter linear – acute, 1 mm long. Hypogynous scales 3 mm long, acuminate. Ovary ellipsoid, sericeous, 1 mm long.

DIAGNOSTIC CHARACTERS

This species may be distinguished from its congeners by its very broadly ovate involucral bracts, glabrous (apart from the ciliate margins) on the outer surface and becoming brown and papyraceous on drying.

Diastella parilis occurs in the upper Breede River Valley where it appears to be confined to a relatively narrow zone along the foothills of the surrounding mountains, at elevations varying from 250 to 500 m on sandy soils derived from Table Mountain sandstone. Seepage areas, which are moist in winter, are the usual habitat. Its range extends from the vicinity of the Tulbagh waterfall southwards to Wolseley and Slanghoek. Flowering takes place over a six-month period, from July to January, during which time the pink inflorescences are produced.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): Ceres road (-AC), Nov., Schlechter 9085 (PRE, PH, BOL, GRA, L, BM, K); Romans River, Sept., Compton 11658 (NBG, BOL); Between Niewekloof and Elandskloof, Jan., Drège s.n. (SAM, BM, S, G, L, K): Roode Sand cascade, Niven 44 (K); Roode Sand, Oct., Roxburgh 39 (K); Darling Bridge (-CA), Sept., Esterhuysen 6091 (BOL, NBG, PRE, K); Slanghoek, July, Walters 258 (NBG); Breede River, July, Walters 149 (NBG); Slanghoek at Goudini (-CB), 7.1.1829, Drège s.n. (P); Goudini Sand flats, 6.1.1829 Drège 1972 (P); on the farm Witelsrivier, Slanghoek valley, July, Rourke 1483 (NBG, PRE, STE, MO).

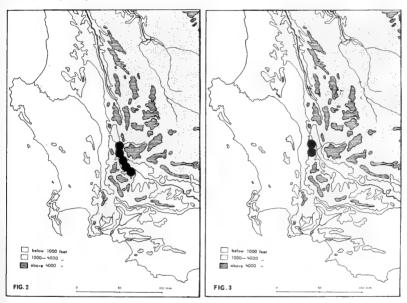
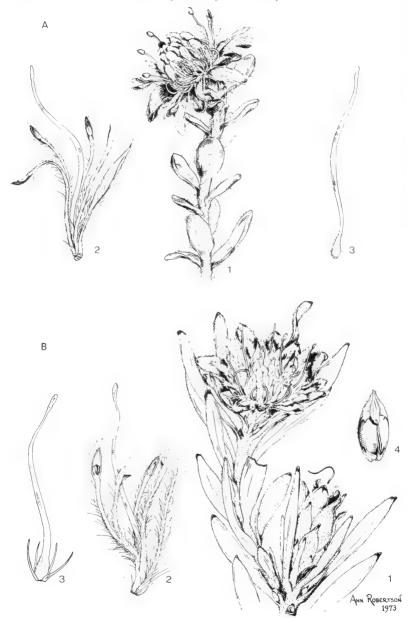


Fig. 2.
Distribution of Diastella parilis Salisb. ex Knight.
Fig. 3.
Distribution of Diastella myrtifolia (Thunb.) Salisb. ex Knight.

(2) Diastella myrtifolia (Thunb.) Salisb. ex Knight, Cult. Prot.: 63 (1809); Phill. & Hutch. in Fl. Cap. 5: 653 (1912).

Protea myrtifolia Thunb., Diss. Prot.: 41 (1718); Fl. Cap., ed. Schultes: 37 (1823). Type: C.B.S., sheet no. 2942 in herb. Thunberg. (UPS!).

Protea dichotoma Lam., Tabl. Encycl. 1: 235 (1792). Type: C.B.S. in herb. Lamarck (P - LA!)



An erect to suberect, densely branched shrub, the lower branches somewhat sprawling; 0.5 - 1 m in height, up to 2 m in diam. *Stems* puberulous, 2 mm in diam. *Leaves* oblong to narrowly elliptic, 1-2.5 cm long, 0.2-0.6 cm wide, usually entire with a single apical callous, occasionally with 2-3 teeth; softly puberulous, becoming glabrescent with age. *Inflorescences* terminal or axillary, usually solitary, but occasionally with up to 3 inflorescences per flowering shoot; broadly campanulate, 1.5 cm in diam. *Involucral bracts* oblong, 5-10 mm long, 1-3 mm wide, foliaceous, sparsely sericeous, margins ciliate, apex obtuse; forming a biseriate, campanulate involucre. *Floral bracts* erect, linear acute, 8-10 mm long, 1 mm wide, densely sericeous. *Perianth* straight 6-8 mm long, the abaxial segment elongating at anthesis, claws sericeous, limbs glabrescent but crinite at apex; tube 2 mm long, glabrescent proximally. *Style* straight or slightly curved, 8 mm long, tapering subterminally. *Pollen presenter* linear, obtuse, 0.5 mm long. *Ovary* ovoid, puberulous, 1 mm long. *Hypogynous scales* linear, subulate. *Fruits* grey, ovoid, 5-6 mm long, 3 mm wide, minutely puberulous.

DIAGNOSTIC CHARACTERS

The presence of hypogynous scales at once characterizes this species which is further distinguished by its oblong-elliptic foliaceous involucral bracts and sprawling, mat-like growth habit.

D. myrtifolia has an exceptionally small area of distribution. Its range extends from the valley around the Tulbagh waterfall in the Kluitjieskraal Forest Reserve, southwards to the Suurvlakte, a distance of about 8 km. Small scattered populations are usually found on sandy soils, particularly on moist seepage areas, near streamsides or in similar damp, sheltered situations, at elevations of from 425 to 600 m. The pink inflorescences are produced mainly from September to January.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): Hills above Tulbagh waterfall (-AC), 29.8.1971, Esterhuysen 32624 (NBG); Tulbagh waterfall valley, 17.1.1894, Guthrie 3117 (NBG); valley above the Tulbagh waterfall, 25.10.1973, Rourke 1400 (NBG); at waterfall, Roodezand, Nov. 1799, Roxburgh 49 (K), by the river and elsewhere in moist places, Roodezand, Oct., Niven 36 (G, PH); Roodezand, Oct., Roxburgh 32 (G); Kluitjieskraal Forest Reserve, Zuurvlakte, Nov., Haynes 219 (STE).

(3) Diastella divaricata (Berg.) Rourke, comb. nov.

Leucadendron divaricatum Berg. in Kongl. Vetensk. Acad. Handl. 27: 322 (1766) – basionym. Type: "e Cap. sp. Grubb" s.n. in herb. Bergius (SBT!)

Fig. 4.

⁽A) Diastella divaricata (Berg.) Rourke ssp. divaricata; (1) flowering shoot × 2,5; (2) open flower × 6; (3) gynoecium × 6 (from Rourke 1490)

⁽B) Diastella myrtifolia (Thunb.) Salisb. ex Knight; (1) flowering shoot × 2,5; (2) open flower × 6; (3) gynoecium – with hypogynous scales × 6; (4) fruit × 3 (from Rourke 1400)

Protea divaricata (Berg.) L., Mant. Alt.: 194 (1771); Thunb., Diss. Prot. 44,58 (1781).

Mimetes divaricata (Berg.) R.Br. in Trans. Linn. Soc. Lond. 10: 111 (1810); Roem. & Schultes, Syst. Veg. 3: 383 (1818); Meisn. in DC., Prodr. 14: 265 (1856).

Diastella serpyllifolia Salisb. ex Knight in Knight, Cult. Prot.: 62 (1809); Phill. & Hutch. in Fl. Cap. 5: 652 (1912); Adamson & Salter; Fl. Cap. Penins.: 326 (1950) – nom. supfl. Type: As for Leucadendron divaricatum Berg.

Diastella vacciniifolia Salisb. ex Knight in Knight, Cult. Prot.: 63 (1809). Type: Specimen labelled "French Hoek Kloof, Niven 45" in Salisbury's hand (K!).

Mimetes parviflora Klotzsch in Krauss, in Flora 28: 77 (1845). Type: In arenosis prope Uitershoek (Cap.), Sept. 1838, Krauss s.n. (isotype NBG, ex Akad. Hohenheim!).

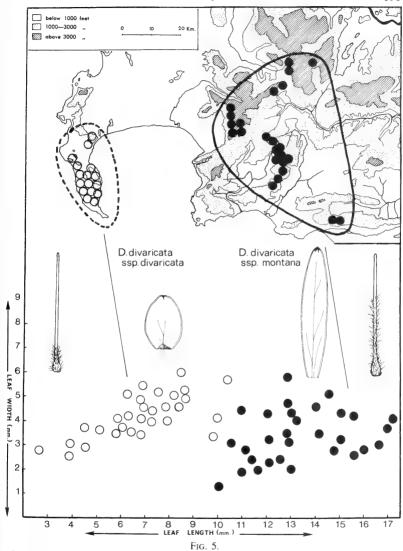
Mimetes intermedia Buek ex Meisn., in DC, Prodr 14: 265 (1856). Syntype: Africa australis, Gueinzius s.n. in herb. Meisner (NY!) N.B. No other syntypes were traced in herb. Meisner.

A low sprawling shrub with a single main stem, forming a tangled mat to 50 cm in height, 1–3 m in diam. *Stems* often trailing, 1–3 mm in diam., pubescent, much branched. *Leaves* ascending or secund to subsecund, oval, ovate, rounded or narrowly lanceolate to lanceolate – elliptic, 2,5–17,5 mm long, 1,5–6,5 mm wide, sparsely villous at first becoming glabrescent to glabrous. *Inflorescences* terminal, globose, 1–1,5 cm in diam. *Involucral receptacle* flat to slightly convex, 1–2 mm in diam. *Involucre* 2 seriate, the same length as the perianth. *Involucral bracts* 5–9 mm long, 1,5–2,5 mm wide, pink at base, greenish towards apex, outer surface sparsely sericeous, margins ciliate. *Floral bracts* 5–8 mm long, filiform, sericeous, pale pink to hyaline. *Perianth* 6–8 mm long, straight, claw and limbs filiform, sericeous; anthers sessile. *Style* straight, filiform, tapering terminally 8–10 mm long, sparsely sericeous on the lower half or less; stigmatic groove terminal. *Ovary* ovoid 1 mm long, sericeous.

REGIONAL VARIATION

From the mass of herbarium material assigned to *Diastella divaricata* it appears possible to detect two forms on the basis of leaf morphology: those with oval, ovate or round leaves and those with narrowly lanceolate to lanceolate-elliptic leaves. In order to make a more objective analysis of the situation, measurements of the leaf dimensions from 30 specimens of each form were plotted as a scatter diagram (Fig. 5).

Two broad groupings, based on leaf length, emerge. Moreover, these groupings can be correlated with leaf morphology and geographical distribution. While no absolutely clear-cut distinction on leaf length is possible, it is clear that the shorter leaf lengths are associated with the round to oval leaved form which is confined to the Cape Peninsula. Longer leaves are associated with the narrowly lanceolate to



Diastella divaricata (Berg.) Rourke, showing distribution and variation. Style pubescence and variation in the leaf dimensions of *D. divaricata* ssp. divaricata are shown on the left (open circles) while style pubescence and variation in the leaf dimensions of *D. divaricata* ssp. montana Rourke are shown on the right (solid circles).

lanceolate-elliptic leaved forms, found in all populations of *D. divaricata* other than those on the Cape Peninsula.

In addition, slight differences in the extent of the pubescence at the base of the style was observed. This too, could be correlated geographically. In populations on the Cape Peninsula, pubescence occurs on the style for a distance of 1–2 mm above the ovary, while in all populations off the Cape Peninsula, pubescence occurs over 5–6 mm of the style above the ovary; that is, on the lower half of the style.

Thus there are slight but constant morphological differences between the two geographical races of D. divaricata. Accordingly, they are here treated as subspecies.

KEY TO THE SUBSPECIES

ssp. divaricata

A low, sprawling shrublet with a densely tangled branch system forming mats to 3 mm in diam. *Leaves* oval, ovate or rounded, 2,5–10 mm long, 2,5–6 mm wide. *Style* sparsely pubescent 1–2 mm above ovary.

DISTRIBUTION

The distribution range of *D. divaricata* ssp. *divaricata* extends over the southern half of the Cape Peninsula from the Steenberg Plateau southwards to Cape Point. It is most abundant at low elevations on the flats although a few populations do occur at elevations of up to 600 m. The small pink inflorescences are produced throughout the year

SPECIMENS EXAMINED

CAPE—3418 (Simonstown): Upper reaches of Bokram stream, Kommetjie, (-AB), Sept., Rourke 1490 (NBG); mountain slopes, Fish Hoek, Jan., Allsopp 41 (PRE); Klawer Valley, Jan., Wolley Dod 300 (BOL, BM, K); Schuster's Bay, Aug., Barker 819 (NBG, PRE); Red Hill, above Simonstown, Boss 348 (PRE, STE); in mountains near Simonstown, Feb., Schlechter 312 (PRE, BM, K, PH); Kalk Bay, Aug., Thode 9287 (STE); Muizenberg, near Steenberg Peak, Aug., Stauffer & Esterhuysen 5042 (PRE, STE); Simons Bay, Oct., R. Brown s.n. (BM); Smiths Farm, Buffels Bay (-AD), Oct., Hutchinson 655 (PRE, BOL, K); Olifantsbos, Jan., Mauve 4247 (PRE, K); Smitswinkel Vlei, June, Morris 97 (NBG); sandy places at Uitershoek, Sept., Krauss s.n. (NBG); near Cape Point, Oct., Godman 859 (BM); Cape Point Nature Reserve, Jan., Rodin 3303 (PRE, K).

ssp. montana Rourke, ssp. nov.

Fruticulus ramosus laxus, teges diffusa formans, 1–2 m in diam. Folia lanceolata-elliptica, 10–17,5 mm longa, 1,5–6 mm lata, apices acuti. Stylus pilosus sparsus 5–6 mm supra ovarium.

A laxly branched, sprawling shrub forming diffuse mats, 1–2 m in diam. *Leaves* narrowly lanceolate to lanceolate-elliptic, 10–17,5 mm long, 1,5–6 mm wide; apices acute. *Style* sparsely pubescent 5–6 mm above ovary.

Type Material: Highlands Forest Reserve, midway between Highlands Forest Station and Houwhoek Pass, 21.11.1973, Rourke 1408 (NBG, holo.; PRE, STE, MO, K, S, iso.)

DISTRIBUTION

As its subspecific epithet indicates, *D. divaricata* ssp. *montana* favours montane habitats, generally at elevations ranging from 300 to 1 200 m. The small, rather scattered populations are usually found in cool, moist, south-east facing situations. Its entire area of distribution, from the Wemmershoek mountains to the French Hoek, Hottentots Holland, Houwhoek and Klein River mountains, falls within a zone that receives light summer precipitation from the cloud banks caused by south-easterly winds, in addition to the usual winter rainfall. Like the typical subspecies, flowering takes place throughout the year.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): Franschhoek Reserve, Purgatory Outspan (-CC), May, *Stehle 156* (STE); Wemmershoek mts, Oct., *Wasserfall 487* (NBG); Louwshoek Peak, west slopes (-CD), Dec., *Esterhuysen 11172* (BOL).

—3418 (Simonstown): Vlakte east of Landdrost Kop (-BB), Dec., *Esterhuysen* 3552 (BOL, PRE); on the path between Landdrost Kop and Somerset Sneeuwkop, March, *Rourke* 1318 (NBG); eastern slopes of Landdrost Kop, June, *Thorne s.n.* (SAM 51549).

—3419 (Caledon): Highlands Forest Reserve, midway between Highlands Forest Station and Houwhoek Pass (-AA), Nov., Rourke 1408 (NBG); Lebanon, at met. station, Jan., Verdoucq 89 (STE, PRE); Houwhoek Forest Reserve, Aug., Hubbard 453 (PRE, STE); in montibus Houwhoek, Zeyher 3694 (STE, PRE, SAM); Houwhoek, Oct., Galpin 4477 (PRE); Lebanon, Nov., Kruger 182 (PRE); Houwhoek Forest Reserve, Sept., Rourke 1108 (NBG); Nuweberg Forest Reserve, Aug., Rourke 828 (NBG); Viljoen's Pass, Dec., Strey 2917 (PRE); Honingklip, Bot River (-AC), Nov., L. E. Taylor 4848 (NBG); Paardeberg, Kleinmond, Nov., Willems 73 (NBG); on the Highlands road, western boundary of Honingklip, July, Rourke 1191 (NBG); Klein River mountains between Hermanus and Stanford (-AD), Sept., Stokoe s.n. (BOL 16891).

(4) **Diastella fraterna** Rourke, sp. nov. *D. divaricata* ssp. *montana* affinis, sed habito suberecto, perianthio lacteo, differt.

Fruticulus parvus, ad 70 cm altus, suberectus. Folia ascendentia vel patentia vel subimbricata, anguste lanceolata-elliptica vel ob lanceolata, 8–14 mm longa, 1–4 mm lata, prope basin torta; sparsim pubescentia vel glabra. Inflorescentiae obconicae-depressae, 1–15 cm in diam., planescentia. Bracteae involucrales 2 seriatae, lanceolatae-ellipticae, obtusae vel acutae, puberulae vel glabrae, 6–10 mm longae, 1–3 mm latae, papyrescentes brunneae; margines ciliatae. Receptaculum 2 mm in diam. Perianthium 8–10 mm longum, rectum, lacteum, sericeum. Stylus rectus, 12–14 mm longus, sparsim sericeous basaliter. Ovarium ovoideum, sericeum, 1 mm longum.

A low shrublet to 70 cm in height, up to 1 m in diam., with a single main stem; erect, or suberect to straggling. *Stems* 1–3 mm in diam., pubescent to glabrous. *Leaves* ascending to patent, occasionally subimbricate; narrowly lanceolate-elliptic to oblanceolate, 8–14 mm long, 1–4 mm wide, occasionally slightly twisted at base; apex acute to obtuse; sparsely sericeous to glabrous. *Inflorescences* obconic – depressed, 1–1,5 cm in diam., becoming flattened on opening. *Involucral bracts* 2 seriate; lanceolate-elliptic, 6–10 mm long, 1–3 mm wide, obtuse, or acute, minutely pubescent to glabrous, drying to brown and becoming papyraceous. *Receptacle* 2 mm in diam., slightly convex. *Floral bracts* linear, sericeous, 1 cm long. *Perianth* 8–10 mm long, white, sericeous; claws linear, limbs acuminate. *Style* straight, 12–14 mm long, very sparsely sericeous in the lower half, tapering terminally. *Anthers* sessile, narrowly lanceolate. *Ovary* 1 mm long, ovoid, sericeous.

Type Material: Paardeberg, above Kleinmond, 19.11.1967, J. P. Rourke 982 (NBG, holo.; PRE, STE, K, MO, iso.)

DIAGNOSTIC CHARACTERS

This species is closely allied to *D. divaricata* ssp. *montana* but may be distinguished from that species by its suberect to erect growth habit and the creamy-white colour of the styles and perianths. Although their distribution ranges are almost contiguous no hybridization appears to take place between the two taxa. In some populations of *D. fraterna* the involucral bracts are particularly distinctive, becoming brown and papyraceous with age.

D. fraterna is confined to the lower Palmiet River valley, ranging from Aries Kraal southwards to the mouth of Palmiet River. Populations occur in a variety of habitats, from sea-level to 450 m. It appears to be equally at home on stony, well-drained slopes and also moist sites such as seepage areas or along stream-sides. Flowering takes place intermittently throughout the year.

SPECIMENS EXAMINED

CAPE—3318 (Simonstown): Between Somersfontein and Aries Kraal, below Kogelberg, (-BB), Jan., *Rourke 1179* (NBG); Palmiet River mountains, lower slopes of Platberg (-BD), April, *Andreae 877* (PRE, STE); Oudebos, Aug., *van*

der Merwe 1229 (STE, PRE); Palmiet River mouth, March, Vogts 10 (PRE, STE); Bobbejaanberg, March, van der Merwe 920 (PRE); stony hills along Palmiet River, April, Esterhuysen 31527; Hangklip, Sept., Compton 13558 (NBG); Palmiet River mouth, Dec., Compton 12821 (NBG).

—3419 (Caledon): Paardeberg, seaward side (-AC), Dec., *Grobler 017* (STE, PRE); 1 km east of Heuningklip, Kleinmond mountains, May, *de Vos 1372* (PRE); road to Kogelberg Reserve from Highlands, Oct., *Williams 532* (BOL); mountains above Kleinmond, Dec., *Rourke 28* (BOL); between Aries Kraal and the Louws River drift, Kogelberg Reserve, Dec., *Rourke 1003* (NBG); Paardeberg, above Kleinmond, Nov., *Rourke 982* (NBG); below "The Crags", Kleinmond, July, *Rourke 785* (NBG); Highlands, Nov., *Compton 12271* (NBG).

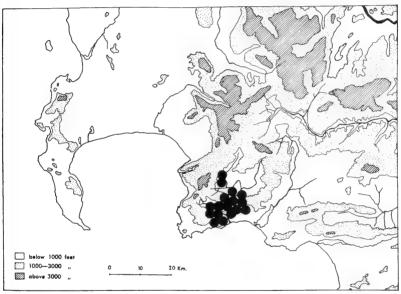


FIG. 6. Distribution of *Diastella fraterna* Rourke.

(5) Diastella thymelaeoides (Berg.) Rourke, comb. nov.

Leucadendron thymelaeoides Berg. in Kongl. Vetensk. Acad. Handl. 27: 324 (1766); Berg., Descript. Plant. Cap.; 19 (1767) – basionym. Type: "e Cap. b spei.", Grubb s.n. in herb. Bergius (SBT!).

Mimetes thymelaeoides (Berg.) R.Br. in Trans. Linn. Soc. Lond. 10: 109 (1810); Roem. & Schult., Syst. Veg. 3: 382 (1818); Meisn in DC., Prodr. 14: 265 (1856).

Protea thymelaeoides (Berg.) Poir. in Lam., Encycl. Meth. Bot. Suppl. 4: 568 (1816).

Protea concava Lam., Tab. Encycl. Meth. Bot. 1: 234 (1792). Type: Cape of Good Hope, without collector, in herb. Lamarck (P-LA!)

Paranomus concavus (Lam.) O. Kuntze, Rev. Gen. Pl. 2: 580 (1891); Levyns in Contrib. Bol. Herb. 2: 39 (1970).

Diastella bryiflora Salisb. ex Knight in Knight, Cult. Prot.: 62 (1809); Phill. & Hutch. in Fl. Cap. 5: 651 (1912) – nom. supfl. type: As for Leucadendron thymelaeoides Berg.

Protea villosa Jacq. ex Meisn. in DC., Prodr. 14: 265 (1856) – as to specimen in herb. Willd. – nom. nud.

An erect to suberect shrub, 0,5–1,5 m in height, with a single main stem. *Stems* 2 mm in diam., densely puberulous, later glabrous. *Leaves* narrowly to broadly oval or broadly elliptic, subimbricate, ascending, entire, with a single apical thickening, puberulous, becoming glabrous, 8–22 mm long, 4–9 mm wide. *Inflorescences* terminal, sessile, globuliform 1–2 cm in diam. *Involucral bracts* 3 seriate, oblong-obtuse, narrowly lanceolate to lanceolate acute, 6–20 cm long, 1–3 mm wide, brown on drying, softly velutinous becoming glabrous later, margins ciliate. *Perianth* 7–10 mm long, straight, densely sericeous but glabrous proximally, creamy-white. Perianth segments free to base. *Floral bracts* linear, 8 mm long, densely sericeous. *Style* sparsely sericeous in the lower half, 10–12 mm long, tapering subterminally. *Pollen presenter* filiform-acute, 0,5 mm long. *Ovary* ovoid, 1 mm long, densely sericeous.

VARIATION

On inspecting all available herbarium material of *D. thymelaeoides*, slight differences in the leaf morphology were evident. It seemed possible to distinguish two groups, one having essentially oval leaves, the other having elliptic leaves. Detailed field studies throughout the distribution area of the species established that specimens of *D. thymelaeoides* having oval leaves tended to occur at the northern end of its distribution range, while collections with elliptic leaves were concentrated at the southern limits of its range. Leaf measurements were made and plotted as a scatter diagram (Fig. 7) in order to examine this apparent trend more objectively.

This revealed that two geographically isolated races of *D. thymelaeoides* are distinguishable: a northern race, centred around the Steenbras catchment area, having short oval leaves, and at the southern end of its range from Rooi Els to Hangklip, a longer-leaved race, having elliptic leaves. While a clear geographical gap, albeit only a small one of about 9 km, exists between these two races, the discontinuity between them that emerges after plotting their leaf dimensions is sufficiently clear to warrant recognition of these two races at the rank of subspecies.

KEY TO THE SUBSPECIES

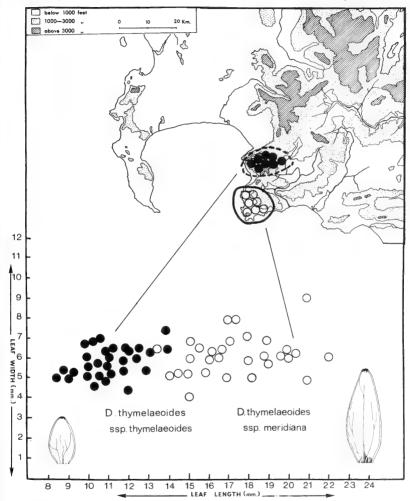


Fig. 7.

Diastella thymelaeoides (Berg.) Rourke, showing distribution and variation in the leaf dimensions of D. thymelaeoides ssp. thymelaeoides (open circles) and D. thymelaeoides ssp. meridiana Rourke (open circles).

ssp. thymelaeoides

An erect shrub to 1,5 m in height. *Leaves* oval or rounded, 8–14 mm long. *Inflorescence* 1–1,5 cm in diam. *Involucral bracts* short, tending to clasp the base of the inflorescence, not prominently stellately patent.

DISTRIBUTION

The typical subspecies occurs chiefly in the Steenbras River catchment area and on the adjacent mountain ranges, at elevations ranging from 450–900 m. Flowering takes place throughout the year but reaches a peak from August to November.

SPECIMENS EXAMINED

CAPE—3418 (Simonstown): Kogelberg (-BB), Aug., *Stokoe* 8377 (BOL); near Steenbras Reservoir, Feb., *Salter* 5212 (BOL, K, NBG); top of Steenbras valley, Jan., *Galpin* 12702 (PRE, K); Steenbras River mountains, Oct., *Andreae* 1149 (PRE); Gordon's Bay, Feb., *Markötter* s.n. (STE 8763); Kogelberg, north-west side, Feb., *Rourke* 326 (NBG); sandy flats east of Steenbras Reservoir, Aug., *Rourke* 823 (NBG); at the head of Boskloof, Steenbras, Aug., *Rourke* 821 (NBG); near Steenbras dam, July, A. B. Rendle 185 (BM); Grabouw, vlei ground, Dec., *Britten* 3125 (PRE): Aries Kraal, Palmiet River valley, Nov., *Lewis* 913 (SAM): Aries Kraal, Nov., *Barker* 3334 (NBG).

ssp. meridiana Rourke ssp. nov.

Frutex suberectus, 0,5–1 m altus. Folia elliptica, 12–22 mm longa. Inflorescentia globuliformis 2 cm in diam. Bracteae involucrales patentes, manifeste stellatae.

A suberect shrub, 0,5–1,0 m in height. *Leaves* elliptic 12–22 mm long. *Inflorescence* globuliform, 2 cm in diam. *Involucral bracts* patent, prominently stellate.

Type Material: Lower north-east foothills of Blesberg, Cape Hangklip 29.6.1975, J. P. Rourke 1482 (NBG, holo; PRE, STE, K, MO, S, M, iso.)

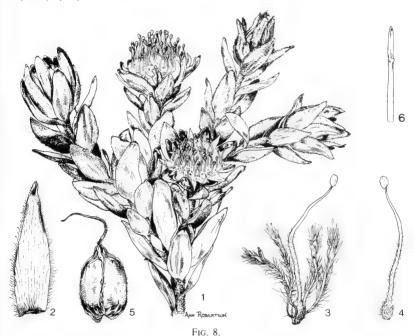
DISTRIBUTION

D. thymelaeoides ssp. meridiana ranges from Rooi Els southwards to Cape Hangklip and Betty's Bay. Unlike the typical subspecies which occupies a montane habitat, the ssp. meridiana is mainly confined to habitats at lower elevations, from sea-level to 150 m. Flowering takes place throughout the year, but mainly from August to November.

SPECIMENS EXAMINED

CAPE—3418 (Simonstown): West base of hill between Pringle Bay and Hangklip (-BD), *Pillans 8228* (K, BOL); Rooi Els, Nov., *Compton 17526* (NBG, BOL, PRE); Pringle East Peak, Sept., *Esterhuysen 18861* (BOL); Hangklip point, Jan., *Rodin 3130* (PRE); Hangklip, north slopes, April, *H. C. Taylor 7069* (STE, PRE);

Betty's Bay, March, *Bayliss 1178* (PRE); Buffelstalberg ridge, May, *Boucher 343* (STE); Rooi Els, May, *Compton 15700* (NBG); The Point, Pringle Bay, Sept., *Rourke 920* (NBG); Hangklip, flats near sea, Dec., *Barker 10365* (NBG); slopes at Pringle Bay, Voorberg, Sept., *Baker 1410* (BM); lower north-east foothills of Blesberg, near Cape Hangklip, July, *Rourke 1482* (NBG, PRE, STE, K, MO, S, M).



Diastella thymelaeoides (Berg.) Rourke ssp. meridiana Rourke; (1) flowering shoot, life-size; (2) involucral bract (inner surface) × 3; (3) open flower with pollen presenter loaded with pollen × 3; (4) gynoecium showing pollen presenter loaded with pollen × 3; (5) mature fruit × 3; (6) style apex and pollen presenter × 12 (from Rourke 1482).

(6) Diastella proteoides (L.) Druce in Rep. bot. Soc. Exch. Club. Br. Isl. 1931 III: 417 (1914).

Leucadendron proteoides L., Sp. Pl. ed. I: 91 (1753); Berg. in Kongl. Vetensk. Acad. Handl. 27: 326 (1766); Berg., Descript. Plant. Cap.: 24 (1767). Lectotype: "Cap. b spei", without collector, No 116.16 in herb. Linn. (LINN!)

Protea purpurea L., Mant. Alt.: 195 (1771); Thunb., Diss. Prot.: 28,51 (1781); Thunb., Fl. Cap.: 129 (1823) – nom. Supfl. Type: As for Leucadendron proteoides L.

Mimetes purpurea (L.) R.Br. in Trans. Linn. Soc. Lond. 10: 111 (1810); Roem. & Schult., Syst. Veg. 3: 383 (1818); Meisn. in DC., Prodr. 14: 266 (1856); var. vulgaris Meisn. in DC., Prodr. 14: 266 (1856). Syntype: Sieber 95 in herb. Meisn. (NY!); var. linnaeana Meisn. in DC., Prodr. 14: 266 (1856). Syntype: Africa australis, Burke s.n. in herb. Meisn. (NY!); var. brevifolia Meisn. in DC. Prodr. 14: 266 (1856). Type: Ex herb. Puerari in herb. Meisn. (NY!).

Mimetes homomalla Reichb.f. ex Meisn. in DC., Prodr. 14: 266 (1856) - nom. nud.

Diastella ericaefolia Salisb. ex Knight in Knight, Cult. Prot.: 64 (1809); Phill. & Hutch. in Fl. Cap. 5: 653 (1912); Adamson & Salter, Fl. of Cape Peninsula: 326 (1950) – nom supfl. Type: As for Leucadendron proteoides L.

A low, sprawling, much divaricate shrub, to 50 cm in height, forming diffuse mats up to 3 m in diam., with a single main trunk; branches horizontally sprawling. Stems 1–2 mm in diam., puberulous, with a short crisped indumentum interspersed with long, straight trichomes. Leaves linear, obtuse, semi-terete, upper surface slightly concave; 5–15 mm long, subsecund to ascending; glabrous or with a few spreading trichomes. Inflorescences 1 cm in diam., sessile, obconic becoming obconic-depressed on opening. Involucre 2–3 seriate. Involucral bracts lanceolate-acuminate, occasionally acute, 5–10 mm long, 1–2 mm wide, outer surface pubescent, inner surface sparsely sericeous proximally, margins ciliate. Floral bracts linear, 5 mm long, hyaline, sericeous. Perianth 7–10 mm long, straight, pink, claws sericeous; limbs lanceolate acute, glabrous; anthers sessile. Style straight, 10 mm long, tapering terminally, lower third minutely pubescent. Pollen presenter linear-acute 0,5 mm long. Ovary ovoid, 1 mm long, sericeous.

DIAGNOSTIC CHARACTERS

D. proteoides may be distinguished from related species by the sericeous pubescence on the outer surface of the involucral bracts and the presence of pubescence on the stems of the current year's growth.

Once abundant on the Cape Flats and in the sandveld to the north of Cape Town, this species formerly occurred along the eastern margin of the Cape Peninsula from Mowbray to Tokai; thence eastwards to Eerste River, Stellenbosch, Kraaifontein and Paarl and northwards as far as Mamre Road station in the north-east and Klein Springfontein in the north-west. At many of these localities it has been exterminated through agricultural or urban development. The distribution map (Fig. 9) therefore shows its former, rather than its present range.

D. proteoides grows on sandy flats in low fynbos, at elevations up to 150 m. This species flowers erratically throughout the year but principally from July to February.

SPECIMENS EXAMINED

CAPE—3318 (Cape Town): Flats 5 miles east of Mamre station (-BC), March, Galpin 12655 (PRE, K); Klein Springfontein, north of Melkbos Strand (-CB),

Sept., Rourke 1094 (NBG); flats near Rondebosch (-CD), Aug., Wolley Dod 617 (BOL, K, BM); Kenilworth, March, Flanagan 2430 (PRE); sandy places near Cape Town, Aug., Marloth 185 (PRE); Claremont flats, Jan., Schlechter 182 (K,L); Cape Flats near Rondebosch, 7.7.1815, Burchell 217 (K); Kenilworth Racecourse, Sept., Barker 4105 (NBG); sandy flats between Katzenberg and Dassenberg (-DA), Oct., Rourke 931 (NBG); on road to Atlantis, near Mamre, Sept., Williams 2065 (NBG); Kalabas Kraal, Jan., Axelson 374 (NBG); Paarl (-DB), Jan., de Villiers s.n. (NBG 104684); high dry ground near Paarl Berg, Oct., Nov., Niven 55 (PH); between Mosselbanks River and Berg River, Paarl, Burchell 979 (K); Wolwefontein, south of Kraaifontein (-DC), March, Oliver 3305 (PRE, STE); Kuils River, Aug., Strey 461 (PRE); between Kraaifontein and

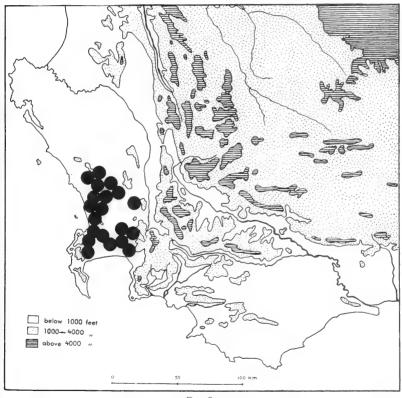


Fig. 9. Distribution of *Diastella proteoides* (L.) Druce.

Bottelary hills, Feb., Rourke 1025 (NBG); Brackenfell, Dec., Compton 10113 (NBG); Joostenberg (-DD), Oct., Esterhuysen 16039 (BOL); Stellenbosch, Duthie 699 (BOL); Muldersvlei, Jan., Pillans 10398 (BR); flats near Joostenberg, Oct., Pillans 16039 (BOL).

—3418 (Simonstown): Wynberg (-AB), *R.C. Alexander Prior s.n.* (PRE); Bergvliet Farm, Oct., *W. F. Purcell s.n.* (SAM); low places near Constantia, Oct., 1801, *R. Brown s.n.* (K); Tokai flats, Oct., *Foley 17* (NBG); Cape Flats near Eerste River (-BB), Dec., *Bolus 2905* (SAM, BM).

(7) Diastella buekii (Gandoger) Rourke, comb. nov.

Mimetes buekii Gandoger in Bull. Soc. bot. Fr. **48**: (1901) – basionym. Type: Africa australis, *Drège* 80226 in herb. Gandoger (LY!) – photo NBG.

Mimetes purpurea (L.) R.Br. var. longifolia Beuk ex Meisn. in DC., Prodr. 14: 266 (1856). Type: "In arenosis circa Franschhoek" Drège s.n. in herb. Meisner (NY.!).

A low prostrate shrub with procumbent trailing stems, forming a dense mat 15 cm in height, up to 1 m in diam. *Stems* glabrous, flushed with red, tending to root at nodes. *Leaves* acicular, 1,0–2,5 cm long, with a thickened apical callous, semi-terete, upper surface occasionally slightly canaliculate; glabrous; ascending or occasionally subsecund to secund. *Inflorescences* borne on short branchlets; obovoid, 1–1,5 cm in diam., overtopped by the surrounding leaves, 15–20 flowered. *Involucral bracts* 2–3 seriate, lanceolate, acute to accuminate, 5–7 mm long, outer surface of outer bracts glabrous, margins ciliate; outer surface of inner bracts sparsely pubescent. *Floral bracts* linear subulate, 6–7 mm long, sericeous. *Perianth* pink, 8–10 mm long; claws straight, sericeous; limbs very narrowly lanceolate acute, glabrous; tube 0,5 mm long. *Style* filiform, to 12 mm, tapering terminally, puberulous above the ovary, the remainder glabrous. *Pollen presenter* 1 mm long, linear acute. *Ovary* ovoid, 1 mm long, puberulous.

DIAGNOSTIC CHARACTERS

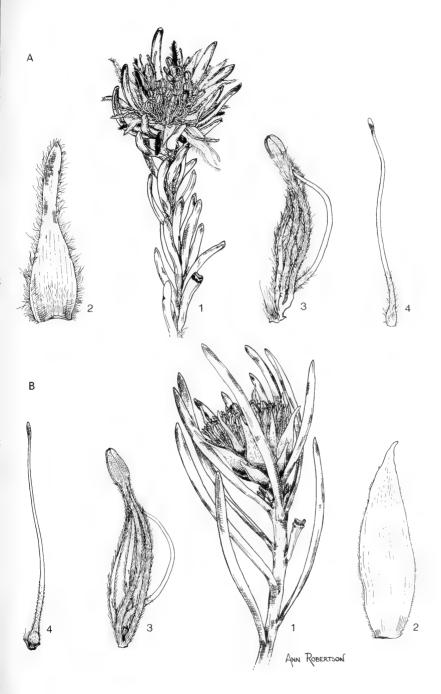
The glabrous acicular leaves, 1-2.5 cm long, overtopping the inflorescence and the distinctly glabrous stems, readily distinguish D. buekii from D. proteoides. In addition, the outer surface of the outer whorl of involucral bracts (apart from the ciliate margins), is glabrous.

Salter and Garside made collections of this species in 1934. Since then, no further material has been deposited in local herbaria. These, as well as the other

Fig. 10.

⁽A) Diastella proteoides (L.) Druce; (1) flowering shoot × 2,5; (2) involucral bract (inner surface) × 6; (3) flower at anthesis × 6; (4) gynoecium × 6 (from Rourke 1094).

⁽B) Diastella buekii (Gandoger) Rourke; (1) flowering shoot × 2,5; (2) involucral bract × 6; (3) flower at anthesis × 6; (4) gynoecium × 6 (from Salter 4731).



collections made earlier this century, are all from roadsides or similarly fragile habitats. Despite several searches at sites where *D. buekii* had been recorded previously, no living plants have yet been traced. It would appear that *D. buekii* must have occurred on the floor of the upper Berg River valley, particularly in the vicinity of the junction of the Berg and Wemmers rivers. It apparently occurred in sandy situations at elevations ranging from 200–300 m. Flowering has been recorded as taking place from August to November.

As the entire area in which *D. buekii* is known to have occurred has now been developed for agricultural and residential purposes, the chances that this species has survived are relatively slim. Nevertheless, although I have not been able to trace any living populations of *D. buekii* it is just possible that a relict population still survives somewhere in the French Hoek valley.

SPECIMENS EXAMINED

CAPE—3318 (Cape Town): Groot Drakenstein (-DD), Nov., F. A. Rogers 17910 (BOL, GRA).

—3319 (Worcester): On sandy wet soil at roadside, La Motte, between main road and Wemmershoek river (-CC), Aug., *Garside* 4621 (K, SAM); slopes of

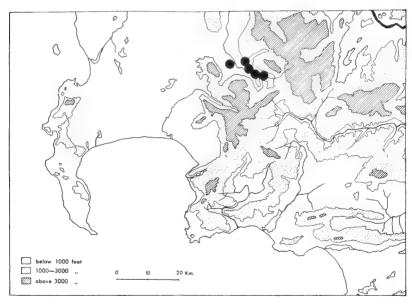


Fig. 11. Distribution of *Diastella buekii* (Gandoger) Rourke.

Drakenstein, French Hoek, Oct., Lamb 2708 (PRE); Wemmers Hoek, Aug., Salter 4731 (K, GRA, BM, NBG, SAM, PRE); sandflats at French Hoek, 5.11.1828, Drège 1490 (P, SAM); French Hoek, Nov., Phillips 1271 (SAM); French Hoek, Nov., Schlechter 9229 (K, L, GRA, PH).

SPECIES NON SATIS COGNITAE

Diastella humifusa Salisb. ex Knight in Knight, Cult. Prot.: 64 (1809); Phill & Hutch in Fl. Cap. 5: 654 (1912). Type: Not traced.

No type of *D. humifusa* has yet been traced. Moreover, Salisbury's description is so vague that it cannot be applied with certainty to any particular population of *Diastella*, although it most closely fits the species here enumerated as *D. buekii*. No clues can be gleaned from the vague information given concerning the type locality: "Mr J. Roxburgh discovered it in Hottentots Holland", according to Salisbury. However tempting it may be to adopt the name *D. humifusa* and apply it to what is here described as *D. buekii*, it is considered wisest to regard *D. humifusa* as imperfectly known until a type specimen comes to light. Despite a careful search in all the major European herbaria known to contain Roxburgh's collections, no type has been unearthed during the past few years and, at this stage, it seems unlikely that it ever will.

Hybrids

Although extensive field work has been undertaken on *Diastella* over many years, the author has never encountered a case of hybridization between species. The only example of hybridization yet detected in nature is a putative bigeneric hybrid between *Leucospermum oleifolium* and *Diastella thymelaeoides*. A single specimen was found growing at Sunny Seas, Betty's Bay, between the two presumed parent species. No other possible parent species were observed in the area. Cuttings of this plant were rooted in a mist propagation unit at the National Botanic Gardens, Kirstenbosch, where they have been cultivated for several years. The hybrid is quite sterile but is exceptionally vigorous. It flowers continuously for almost six months, making a fine horticultural subject. At this stage it can only be suggested that this plant is a putative bigeneric hybrid on the basis of its gross morphology. A detailed cytological study will have to be undertaken in due course in order to confirm this supposition.

Leucospermum oleifolium × Diastella thymelaeoides

CAPE—3418 (Simonstown): Sunny Seas, Betty's Bay (-BD), a single plant seen, 7.1.1965, Kourke 245 (NBG).

ACKNOWLEDGEMENTS

In 1968 while holding the Smuts Memorial Fellowship in Botany, the author was able to make personal visits to many major European herbaria in order to examine type material. I am greatly indebted to the University of Cape Town for

the award of this fellowship and to the directors of all the herbaria, whose specimens are cited in this paper, for making their collections freely available to me.

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AN ECOLOGICAL STUDY OF THE DUNE FOREST AT MAPELANA, CAPE ST LUCIA, ZULULAND*

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ABSTRACT

A quantitative account of the composition of the Dune Forest at Mapelana is given. The prevailing environmental conditions and their influence on the vegetation are also briefly discussed.

UITTREKSEL

'N EKOLOGIESE STUDIE VAN DIE DUINWOUD VAN MAPELANA, KAAP ST LUCIA, ZULULAND*

'n Kwantitatiewe verslag van die samestelling van die duinwoud van Mapelana word aangebied. Die heersende omgewingsfaktore en die invloed daarvan op die plantegroei word ook kortliks bespreek.

Introduction

The Mapelana Forest, of which a small portion is to be seen in Fig. 1, is situated just north of Cape St Lucia (Fig. 2). The dunes on which the Forest grows, are approximately 2 km wide and up to 188 m high (Hobday, 1955). The dunes are adjacent to the coast and run parallel to it in a north-east/south-west direction.

The Department of Forestry has jurisdiction over most of the area, while the Natal Parks Board has an anglers' reserve at the northern boundary of the forest. Between these two bodies the forest is protected so effectively that very little disturbance was noticeable at the time of the investigation.

PHYSIOGRAPHY AND CLIMATIC FACTORS

The forest soil consists of unconsolidated brown sand. The mean moisture content of the top soil at field capacity is 12,7 per cent of the dry mass. The permanent wilting point is only a little lower, viz. 10,8 per cent of the dry mass. The moisture available to plant growth is thus very low, and wilting of the forest floor plants in particular is quickly detectable during a slightly prolonged dry spell. The pH of the forest top soil lies between 6,7 and 7,4 and the organic matter content varies from 4,6 to 6,2 per cent of the dry mass of the soil.

^{*}This article forms part of a thesis submitted by H. J. T. Venter for the D.Sc. degree in General Botany at the University of Pretoria. Accepted for publication 18th February, 1976.

The temperatures of the area are high in summer with a mean of 26,1 days per annum above 30°C; the extreme maximum recorded is 38,9°C. The winters are moderate, the lowest monthly mean being 13,4°C; the extreme minimum recorded is 5,7°C. The relative humidity is high with a monthly mean at 08h00 of between 79 and 88 per cent and at 14h00 between 61 and 74 per cent. From May to August



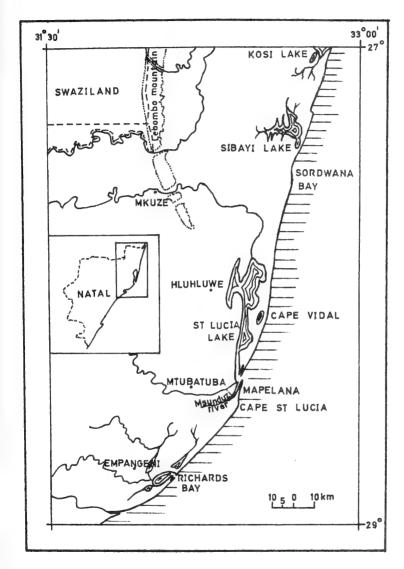
Part of the hinddune forest viewed from the west. In the foreground *Barringtonia* racemosa and *Ficus sycomorus* can be distinguished.

the relative humidity may drop below 70 per cent. The mean annual rainfall for this area is 1 287,9 mm. Sixty per cent of the total falls between October and March, with the peak in March when a mean of 204,2 mm is measured. From these data it may be deduced that a humid-subtropic climate favourable for plant growth prevails (Weather Bureau, 1954 & 1955).

METHODS OF SURVEY

In order to obtain an indication of the limits of the different forest zones and of the canopy trees characterizing them, transects traversing the dunes were laid out.

Due to the extreme density of the forest line transects with survey points at intervals of 10 paces were used. The area around every survey point was divided into quadrants. In each quadrant the tree species nearest to the survey point and of which the trunk diameter at breast height measured at least 10 cm, was listed. This minimum diameter ensured that mainly canopy-tree species which characterize the different forest zones were included. From the data obtained, histograms were



 $F_{IG.\ 2}.$ Locality map of the coast belt of Zululand.

compiled and from these figures the various zones or stands of the forest were delimited on the foredunes and the hinddunes.

Apart from the transect sudies, a quantitative investigation was made of the hinddune forest to determine its composition. The survey was carried out according to the method of Cottam & Curtis (1959) and Curtis & Cottom (1964) whereby the canopy, subcanopy and lianas were studied with the quarter technique, and the herb stratum by quadrats. This plotless quarter method was adopted because of the extremely dense growth of the Mapelana Forest.

The criteria used in the present study to distinguish between the different strata are as follows:

Canopy stratum – Tree species of the forest canopy of which the trunk diameter at breast height (1,5 m above ground-level) measures at least 10 cm.

Subcanopy stratum – Tree and shrub species which never form part of the canopy stratum and of which the trunk diameter at breast height measures at least 2,5 cm. Saplings of the canopy species with trunk diameters of 2,5 to 10 cm at breast height are included in the subcanopy.

Herb stratum - Herbs, woody herbs, herbaceous climbers and seedlings of the canopy, subcanopy and lianas.

Lianas – Those woody climbers which reach at least the canopies of the trees of the subcanopy stratum.

Three surveys were made along the foot, slope and crest of the hinddune respectively. Each survey comprised 40 stratified points which were 10 paces apart on a single line of 400 paces long, placed roughly on a specific contour line of the dune. At each point the ground area was divided into quadrants and a quadrant of $1\ m^2$ was consistently located in the same position in relation to the point.

In each quadrant the tree species which grew nearest to the point, and which complied with the stipulated criteria for the canopy stratum, was listed. The basal area of the tree was measured at breast height with a basal area tape, and the height was measured with a range finder. A survey of 40 points thus provided data on 160 trees. A distance of 10 paces between consecutive points normally ensured that the same individual tree was not sampled more than once. If this, however, happened then the tree second nearest to the point was chosen.

The same procedure was followed for the lianas and the subcanopy, except that the height of the lianas was not measured and no basal area or height was measured in the case of the subcanopy species.

For the herb stratum the species present in the 1 m² quadrats, were listed.

The data of the three separate surveys were finally combined into one comprehensive set of data. From these data importance values (IV) were determined as follows:

Canopy species: IV = (RF + RD + RDo)/3 per cent Liana species: IV = (RF + RD + RDo)/3 per cent Subcanopy species: IV = (RF + RD)/2 per cent

Herb stratum species: IV = RF per cent.

RF = Relative frequency, e.g. the number of occurrences of one species as a percentage of the total number of occurrences of all species.

RD = Relative density, e.g. the number of individuals of one species as a percentage of the total number of individuals of all species.

RDo = Relative dominance, e.g. the total basal cover of one species as a percentage of the total cover of all species.

In addition to the above values, the density per hectare (D/ha) was determined for the canopy, subcanopy and lianas. Basal cover per hectare (BC/ha) was determined for the canopy stratum only.

RESULTS AND DISCUSSION

The investigation revealed clearly that the Mapelana Forest comprises two distinct communities, viz. a sea-facing foredune community that is conspicuously affected by salt-spray from the sea and an inland-facing hinddune community where the influence of salt-spray is not obvious. Bayer and Tinley (1965) drew a similar distinction.

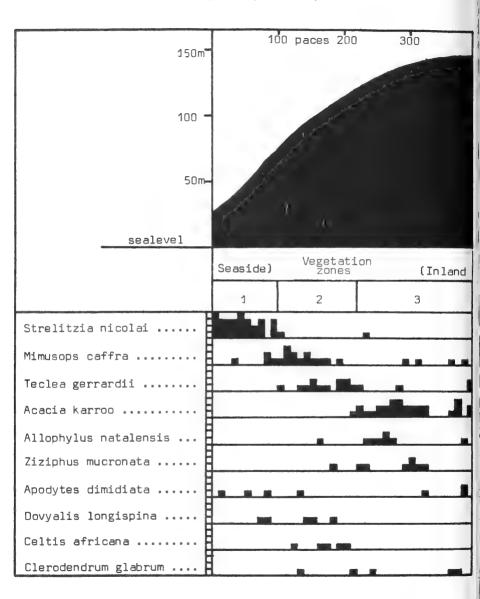
The condition is not restricted to the Mapelana Forest, but is present all along the coast of Natal wherever high sand-dunes occur, for example at Richards Bay and Sibayi Lake (Venter, 1973), Cape Vidal (personal observation, 1972) and Hawaan Forest (Moll, 1968).

The foredune community

The foredune community at Mapelana is not uniform in composition. Two main types of salt-spray forest are present. The most extensive of the two is characterized by the dominance of *Strelitzia nicolai*, *Mimusops caffra* and *Acacia karroo* (Fig. 3). *Strelitzia nicolai* is totally dominant just above the beach of wind-swept sand. It forms such an impenetrable growth that few other species apart from *Mimusops caffra* are observable. Above the zone of *Strelitzia nicolai* the forest becomes more mixed in composition with *Mimusops caffra* the dominant and *Teclea gerrardii* the subdominant. *Allophylus natalensis*, *Ziziphus mucronata*, *Dovyalis longispina* and *Apodytes dimidiata* are regularly encountered.

Although Acacia karroo represents the third zone in Fig. 3, this species is not present as a continuous belt along the foredune, but is more or less restricted to the borders of smaller patches or larger areas of grassland or blow-sand near or at the top of the dune. In places where the Acacia karroo zone is absent, the Mimusops caffra vegetation continues over the crest of the foredune to link up with the forest of the hinddune.

The second type of salt-spray forest at Mapelana is very dense, low-growing brushwood of *Diospyros rotundifolia*, *Mimusops caffra*, *Brachylaena discolor*, *Eugenia gueinzii*, *Ficus burtt-davyi* and *Euclea schimperi*.



The influence of the wind-blown salt-spray from the sea is distinctly demonstrated in this brushwood forest. Succulence of the foliage is very common. According to Boyce (1954) this condition is induced by a gradual accumulation of chloride ions in the leaves which eventually results in hypertrophic growth of the parenchyma cells. Most conspicuous, however, is the tangled growth form and evenly pruned canopies of the trees and shrubs. These conditions are direct results of salt-spray poisoning which kills off the terminal and other buds of stems exposed to salt-spray.

The hinddune community

This community does not reveal any observable symptoms of salt-spray poisoning. The steep and high foredune obviously protects the hinddune from salt-spray contamination. Venter (1973) found at Richards Bay that there is a marked drop in salt-spray intensity from the foredune to the hinddune area and that only a very low quantity is detectable at 1 000 m from the beach with no visible poisoning in the vegetation at this distance.

The zonation of the hinddune forest is indicated in Fig. 4. On the landward side a clearly demarcated belt of swampy, clayey alluvium is located between the foot of the dune and the Msunduzi River (zone 1 in Fig. 4). Ficus sycomorus and Barringtonia racemosa are more or less exclusive but individuals of Hibiscus tiliaceus, Rauvolfia caffra, Voacanga thouarsii and Ficus hippopotami are also present. (The last mentioned species is the dominant tree in the vast swamp of Cyperus papyrus on the inland side of the Msunduzi River.) The Ficus sycomorus trees are huge emergents up to 19 m tall (Fig. 1) and have typical buttressed trunks. Barringtonia racemosa in contrast, never acquires such dimensions, but is present in such large numbers that it forms one continuous, dense subcanopy below Ficus sycomorus. Many seedlings and saplings of Barringtonia racemosa are present in the understorey which indicates that this species reproduces itself actively under the prevailing conditions.

On the seaward edge of the hinddune forest *Mimusops caffra* and *Acacia karroo* are the most important species (Fig. 4, zone 3). This zone borders on the already mentioned extensive area of grassland and blow-sand that separates the forest of the foredune from that of the hinddune. In places, however, the foredune and hinddune communities have converged into one continuous belt of forest across the dunes.

Acacia karroo is apparently invading the grassland and blow-sand, but once it has formed dense stands, none of its seedlings are to be observed, probably

Fig. 3.

Histogram of the foredune forest at Mapelana representing the distribution of the main tree species from the beach to the grassland on top of the dunes. (The histogram is compiled from a line transect of 40 points, every two points 10 paces apart. One division of the vertical scale represents 25 per cent frequency at a survey point.)

because this species is a heliophyte. The result of its absence in the lower strata is that Mimusops caffra and Celtis africana invade the stands of Acacia karroo and eventually replace it. Breen (1971) similarly found little evidence of regeneration of Acacia karroo in its stands in the dune forest at Lake Sibayi. Surprisingly he also found no saplings or seedlings of other forest species present in these stands. A possible explanation for this may be that the stands of Acacia karroo at Lake Sibayi were still so young that conditions were not yet favourable for the appearance of other species. Venter (1973) studied stands of various ages at Richards Bay and found other tree species to appear in older stands of Acacia karroo.

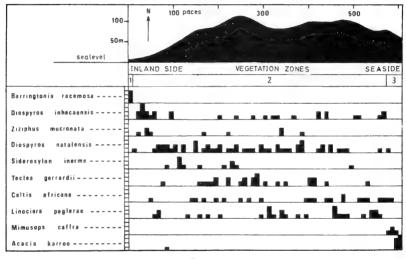


Fig. 4.

Histogram of the hinddune forest at Mapelana representing the distribution of the main tree species from the Msunduzi River across the dunes to the grassland on the seaward side of the forest. (The histogram is compiled from a line transect of 62 points, every two points 10 paces apart. One division of the vertical scale represents 25 per cent frequency at a survey point.)

Observations of this border zone furthermore suggest that also *Mimusops caffra* eventually disappears from the forest and that it acquires a more mixed composition of *Diospyros natalensis*, *Celtis africana*, *Strychnos madagascariensis*, *Teclea gerrardii* and *Linociera peglerae* as illustrated in Fig. 4, zone 2. Thus there apparently exists a sequence of successional stages as forest vegetation invades grassland and blow-sand on the dunes. Similar trends are to be observed elsewhere along the coast of Zululand (Venter, 1973).

The major portion of the forest covering the foot, western slope and crest of the hinddune is dominated by *Diospyros natalensis* (Fig. 4, zone 2). As described under "Methods of Survey", a comprehensive quantitative survey was made in this forest and the results are summarized in Tables 1 to 5.

Diospyros natalensis is the most conspicuous species and has an importance

TABLE 1.

Relative frequency, density and dominance, importance values, basal cover and density per hectare of the canopy species of the *Diospyros natalensis* community.

(Summary of the data of a survey of 160 points)

	RF	RD	RDo	IV	BC/ha (m²)	D/ha
Diospyros natalensis	19,7	26,2	15,1	20,3	5,96	182
Celtis africana	8,9	8,9	13,0	10,3	5,13	62
Strychnos madagascariensis	7,3	7,7	11,5	8,8	4,54	54
Linociera peglerae	8,5	7,7	5,0	7,1	1,97	54
Ziziphus mucronata	4,8	4,2	12,2	7,1	4,81	29
Teclea gerrardii	7,8	7,3	3,7	6,3	1,46	51
Sideroxylon inerme	5,8	5,4	6,7	6,0	2,64	39
Diospyros inhacaensis	6,3	5,8	4,7	5,6	1,85	41
Chaetacme aristata	2,9	2,5	4,3	3,2	1,70	17
Cassine papillosa	3,3	3,1	3,3	3,2	1,30	22
Dovyalis longispina	4,1	3,4	1,8	3,1	0,71	24
Apodytes dimidiata	1,8	1,7	3,4	2,3	1,34	12
Eugenia natalitia	2.9	2.5	1,1	2,2	0,42	17
Drypetes natalensis	2,2	1,9	0,7	1,6	0,28	13
Cassine aethiopica	1,8	1,5	1,3	1,5	0,51	10
Euclea schimperi	1,8	1,7	1,0	1,5	0,39	12
Olea capensis subsp. macrocarpa	1,0	1,0	2,0	1,3	0,79	7
Ficus polita	0,5	0,4	2,6	1,2	1,03	3
Mimusops caffra	1,0	0,8	1,2	1,0	0,46	6
Plectroniella armata	1,3	1,0	0,4	0,9	0,16	7
Mimusops obovata	0,5	0,4	1,5	0,8	0,58	3
Cussonia sphaerocephala	0,5	0,4	1,0	0,6	0,39	3
Inhambanella henriquesii	0,9	0,8	0,2	0,6	0,08	6
Acacia karroo	0,7	0,6	0,3	0,5	0,12	4
Bersama lucens	0,5	0,4	0,2	0,4	0,08	3
Cassipourea gerrardii	0,5	0,4	0,2	0,4	0,08	3
Maytenus nemorosa	0,5	0,4	0,2	0,4	0,08	3
Clausena anisata	0,5	0,4	0,1	0,3	0,04	3
Ficus natalensis	0,2	0,2	0,6	0,3	0,24	1
Canthium ventosum	0,2	0,2	0,2	0,2	0,08	I
Celtis durandii	0,2	0,2	0,2	0,2	0,08	1
Cordia caffra	0,3	0,2	0,1	0,2	0,04	1
Turraea floribunda	0,3	0,2	0,2	0,2	0,08	1
T. obtusifolia	0,2	0,2	0,1	0,2	0,04	1
Total	99,7	99,7	100,1	99,8	39,46	696

Tree height: mean for the community 9,7 m maximum for the community 19,5 m

value of 20,3 per cent in the canopy stratum (Table 1). Although this species does not attain the size of the emergent species such as $Ziziphus\ mucronata$ it has such a high density that its total basal cover of 5,96 m²/ha exceeds that of every other species present (Table 1).

Celtis africana is the subdominant of the community and has an importance value of 10,3 per cent. This species is also widespread through the forest, but is less common on the steep slope.

Other important component species of the canopy stratum are *Strychnos madagascariensis*, *Linociera peglerae*, *Teclea gerrardii*, *Ziziphus mucronata*, *Sideroxylon inerme* and *Diospyros inhacaensis*. These species have importance values that range from 8,8 to 5,6 per cent (Table 1).

Although not apparent from Table 1, the three separate surveys of the foot, slope and crest of the dune indicated that *Diospyros inhacaensis* is more common at the foot, *Sideroxylon inerme* attains its highest value on the slope and *Ziziphus mucronata* is most common at the foot and crest but is nearly absent from the slope. These distribution patterns may be caused by a less favourable moisture régime on the steep slope where loss due to runoff is likely to be higher than at the foot and crest. Venter (1973) found a comparable distribution pattern in the dune forest at Lake Sibayi where *Ziziphus mucronata* and *Diospyros inhacaensis* are dominant along the dune foot, but absent from the slope, while *Sideroxylon inerme* is an important member of the slope forest, but not so at the foot.

The density of the canopy stratum amounts to 696 trees/ha which is considerably more than the mean totals of 496 and 504 trees/ha determined respectively for the Hawaan and Hlogwene dune forests by Roger and Moll (1975). (These authors' criteria for canopy and subcanopy together equal the criterium for the canopy in the present study.) Venter (1973) found the mean densities for the canopy stratums of the dune forests at Lake Sibayi and Richards Bay to be 478 and 385 respectively. The high density may be attributed to climatic factors which are obviously more favourable at Mapelana than at any other locality along the coast of Natal. The mean annual precipitation at Cape St Lucia for example, amounts to 1 287,9 mm/annum, compared to 1 105,8; 934,8; 947,8 and 923 mm/annum respectively at Richards Bay, Maputa (Kosi Bay), Mbazwane (Lake Sibayi) and Mt Edgecombe in the vicinity of the Hawaan forest (Venter, 1973, Breene, 1971, and Moll, 1968).

The basal cover of the canopy stratum totals $39,46 \text{ m}^2/\text{ha}$. Again this value is high if compared to the values of 31,94 and $23,56 \text{ m}^2/\text{ha}$ measured at Richards Bay and Lake Sibayi respectively (Venter, 1973). This is also higher than the values of 34,88 and $24,90 \text{ m}^2/\text{ha}$ measured at Hawaan and Hlogwene forests respectively by Roger and Moll (1975).

The mean height of the forest canopy is 9,7 m (Table 1), but large emergents occur frequently, especially at the dune foot. The maximum height that was measured, was 19,5 m for an individual of *Mimusops caffra*.

TABLE 2.

Relative frequency and density, importance values and density per hectare of the subcanopy species in the *Diospyros natalensis* community.

(Summary of the data of a survey of 160 points)

	RF	RD	IV	D/ha
Diospyros natalensis*	13,4	15,2	14,3	189
Psychotria capensis	12,2	15,9	14,1	198
Drypetes natalensis*	8,3	8,3	8,3	103
Deinbollia oblongifolia	5,4	5,9	5,7	73
Linociera peglerae*	5,6	5,7	5,7	71
Pancovia golungensis	5,1	5,2	5,2	65
Dovyalis longispina*	5,1	4,3	4,7	53
Eugenia natalitia*	4,6	4,4	4,5	55
Dracaena hookeriana	4,5	4,3	4,4	53
Vangueria chartacea	4,2	3,8	4,0	47
Clausena anisata	2,4	2,0	2,2	25
Teclea gerrardii*	2,3	2,0	2,2	25
Celtis africana*	2,3	1,9	2,1	24
Strychnos madagascariensis*	1,8	1,9	1,9	24
Diospyros inhacaensis*	2,0	1.6	1.8	20
Carissa bispinosa	1,8	1,6	1,7	20
Cassine papillosa*	1,5	1,5	1.5	19
Plectroniella armata*	1,3	1,2	1.3	15
Pavetta revoluta	1.3	1,0	1,2	12
Sideroxylon inerme*	1,3	1,1	1.2	14
Inhambanella henriquesii*	1,1	0,9	1,0	12
Maytenus nemorosa	1.0	0,8	0.9	10
Peddiea africana	1,0	0,8	0.9	10
Acalypha glabrata	0,7	0,6	0,7	7
Tricalysia sonderiana	0,7	0,6	0.7	7
Turraea obtusifolia	0,8	0,6	0.7	7
Xeromphis rudis	0,7	0,6	0,7	7
Cassine aethiopica*	0,5	0,6	0,6	7
Bequaertiodendron natalense	0,5	0,4	0,5	5
Euclea schimperi*	0,5	0,4	0,5	5
Mimusops caffra*	0,5	0,4	0,5	5
Turraea floribunda	0,5	0,4	0,5	5
Bersama lucens*	0,2	0,2	0,2	3
Brachylaena discolor	0,2	0,2	0.2	3
Canthium ventosum	0,2	0.2	0,2	3
Clerodendrum glabrum*	0,2	0.2	0,2	3
Euclea natalensis*	0,2	0,2	0,2	3
Ficus polita*	0,2	0,2	0,2	3
Gardenia thunbergia	0,2	0,2	0,2	3
Grewia occidentalis	0,2	0,2	0,2	3
Heywoodia lucens*	0,2	0,2	0,2	3
	0,2	0,2	0,2	3
Kraussia floribunda	0,2	0,2	0,2	3
Mimusops obovata* Mitriostigma axillare	0,2	0,2	0,2	3
9	0,2	0,2	0,2	3
Pavetta delagoensis	0,2	0,2	0,2	3
Strychnos decussata*				3
Trichilia emetica*	0,2	0,2	0,2	3
Ziziphus mucronata*	0,2	0,2	0,2	3
Total	98,1	99,1	99,4	1 240

^{*}Canopy species.

As in the case of the canopy stratum, *Diospyros natalensis* is once more dominant in the subcanopy with an importance value of 14,3 per cent (Table 2). *Psychotria capensis* has an equally high value of 14,1 per cent. *Diospyros natalensis*, however, is important throughout the community, while *Psychotria capensis* attains importance only at the summit and foot of the dune and is not encountered on the slope.

Pyrecantha scandens, Rhoicissus sp. and Scutia myrtina are the most common liana species present. They have importance values of respectively 16,1; 12,7 and 11,1 per cent (Table 3). On the basis of basal cover, however, Scutia myrtina and

TABLE 3.

Relative frequency, density and dominance, importance values and density per hectare of the liana species in the *Diospyros natalensis* community.

(Summary of the data of a survey of 160 points)

	RF	RD	RDo	IV	D/ha
Pyrenacantha scandens	20,0	24,0	4,2	16,1	488
Rhoicissus sp	12,3	17,1	8,8	12,7	348
Scutia myrtina	6,1	4,7	22,4	11,1	96
Grewia caffra	4,5	4,1	20,5	9,7	83
Acacia kraussiana	9,8	8,9	5,5	8,1	181
Cissus fragilis	7,8	7,7	1,6	5,7	157
Pergularia daemia	6,1	5,5	2,9	4,8	112
Grewia occidentalis	2.4	2,0	8,4	4,3	41
Uvaria caffra	4,2	4,0	4,3	4.2	81
Rhoicissus tomentosa	1,2	1,8	5,4	2,8	37
Asparagus falcatus	4.0	3.0	1,2	2,7	61
A. setaceus	3,6	3.2	0.7	2.5	65
Capparis fascicularis	2,7	2.0	2.6	2,4	41
Adenia gummifera	1.2	0.9	3.5	1.9	19
Pisonia aculeata	1.2	0.8	3.1	1.7	16
Rhus natalensis	1,6	1.7	1.8	1.7	35
Tinospora caffra	1.6	1.1	0.5	1.1	22
Cyphostemma cirrhosum	1,5	1.1	0,2	0,9	22
Hippocratea schlechteri	0.9	0.8	0,3	0.7	16
Ceropegia grandis	0,8	0.8	0,3	0,6	16
Brachylaena discolor	0,6	0,4	0,4	0,5	8
Secamone frutescens	0,8	0,7	0,1	0,5	14
Allocassine laurifolia	0,6	0,4	0,1	0,4	8
Cynanchum ellipticum	0,6	0,4	0,1	0,4	8
Jasminum streptopus	0,6	0,4	0,1	0,4	8
Senecio mikanioides	0,6	0,4	0,1	0,4	8
Vernonia angulifolia	0,6	0,4	0,1	0,4	8
Tragia rupestris	0,6	0,4	0,1	0,4	8
Monanthotaxis caffra	0,5	0,4	0,1	0,3	8
Maerua racemulosa	0,3	0,2	0,4	0,3	4
Cissampelos torulosa	0,3	0,2	0,0	0,2	4
Dioscorea sylvatica	0,3	0,2	0,0	0,2	4
Tylophora anomala	0,3	0,2	0,0	0,2	4
Total	100,2	99,9	99,8	100,3	2 031

Grewia caffra outranks all the other liana species by far with relative dominance values of 22,4 and 20,5 per cent respectively.

These last-mentioned two species very obviously constitute an important component of the forest-canopy stratum. The canopies of these two climbers become so massive that one often observes broken trees where the mass of these two species had become so excessive that the supporting tree branches had torn off and the whole canopy, tree and liana, dropped to the forest floor. Strong winds, of course, may play a part in this destruction. In these places, where the forest-canopy has opened up, more sunlight penetrates to the herb stratum and this results in a spectacular upsurge of seedlings and saplings.

Not many of the lianas present attain impressive stem dimensions, even though they reach up into the forest canopy. The maximum stem diameters measured

Table 4. True and relative frequency of the herb stratum species of the $Diospyros\ natalensis$ community. (Summary of the data of 160 quadrats of 1 m² each)

	TF**	RF
Isoglossa woodii	58,3	11,1
Diospyros natalensis*	55,8	10,6
Psychotria capensis	30,8	5,8
Eugenia natalitia*	25,0	4,8
Teclea gerrardii*	24,2	4,6
Linociera peglerae*	22,6	4,3
Drypetes natalensis*	20,0	3,8
Clausena anisata	19,2	3,6
Dracaena hookeriana	18,3	3,5
Acacia kraussiana	14,2	2,7
Asparagus falcatus	13,3	2,5
Pyrenacantha scandens	13,3	2,5
Phymatodes scolopendria	12,5	2,4
Oplismenus hirtellus	11,7	2,2
Uvaria caffra	11,7	2,2
Cyperus albostriatus	10,8	2,1
Hippocratea schlechteri var. peglerae	10,8	2,1
Asparagus setaceus	9,2	1,7
Capparis fascicularis var. zeyheri	8,3	1,6
Deinbollia oblongifolia	8,3	1,6
Drimiopsis maculata	6,7	1,3
Cissus fragilis	6,7	1,3
Pupalia atropurpurea	6,7	1,3
Sansevieria guineensis	6,7	1,3
Strychnos madagascariensis	6,7	1,3
Cyphostemma cirrhosum	5,8	1,1
Pavetta revoluta	5,8	1,1
Pancovia golungensis	5,8	1,1
Carissa bispinosa var. acuminata	4,2	0,8
Peddiea africana	4,2	0,8
Allophylus melanocarpus	3,3	0,6
Gardenia thunbergia	3,3	0,6

	TF**	R
Cassine aethiopica*	2,5	0.
Celtis africana*	2,5	0.
Coleotrype natalensis	2,5	0.
Commicarpus africanus	2,5	0,
Mimusops obovata*	2,5	0,
Plectroniella armata*	2,5	0.
Secamone frutescens	2,5	0,
Tragia rupestris	2,5	0.
Vangueria chartacea	2,5	0.
Vernonia angulifolia	2,5	0.
Acalypha glabrata	1,7	0.
Anthericum saundersiae	1,7	0.
Bequaertiodendron natalense	1,7	0,
Ceropegia grandis	1,7	0,
Chaetacme aristata*	1,7	0.
Ctenomeria capensis	1,7	0.
Dioscorea cotinifolia	1,7	0,
Diospyros inhacaensis*		
Fricalysia lanceolata	1,7	0,
	1,7	0,
Keromphis rudis	1,7	0,
Ziziphus mucronata*	1,7	0,
Achyranthes sicula	0,8	0,
Allocassine laurifolia	0,8	0,
Asplenium prionitis	0,8	0,
Bersama lucens*	0,8	0,
Cassine papillosa*	0,8	0,
Commelina benghalensis	0,8	0,
Cynanchum ellipticum	0,8	0,
Euclea schimperi var. schimperi*	0,8	0,
Grewia occidentalis	0,8	0,
Haemanthus sp. (HJTV 6139)	0,8	0,
Laportea peduncularis	0,8	0,
Aaytenus mossambicensis var. mossambicensis	0,8	0,
Ochna natalitia*	8,0	0,
Pavetta delagoensis	0,8	0,
Pergularia daemia	0,8	0,
Rhoicissus sp. (HJTV 5549)	0,8	0,
Rhynchosia cf. R. caribaea	0,8	0,
Senecio mikanioides	0,8	0,
Tricalysia sonderiana	0,8	0,
Turraea obtusifolia	0,8	0,
Vernonia anisochaetoides	0,8	0,
Species (<i>HJTV 5510</i>)	0,8	0,
Total		101,

^{*}Canopy species. **TF = True frequency.

were 12 and 11 cm (at breast-height) for *Scutia myrtina* and *Grewia caffra* respectively. The majority of the climbers have stem diameters of less than 1 cm.

A large variety of species grow in the herb stratum (Table 4). *Isoglossa woodii*, a woody acanthaceous herb, is most conspicuous and without a doubt exerts a dominating influence on the forest vegetation. Wherever present, this species grows into an extremely dense cover of up to 3 m high. Its canopy becomes so dense that hardly any sunlight filters through to the forest floor where other smaller plants and tree seedlings are present. It was observed that *Isoglossa woodii* is especially abundant in shade, but it may be as abundant in exposed patches.

TABLE 5.
Epiphytes and their supporting plants in the *Diospyros natalensis* community. (Summary of the data obtained during the survey of 160 points)

				suppo	orting p	lants			
	Acacia kraussiana	Chaetacme aristata	Diospyros inhacaensis	Diospyros natalensis	Eugenia natalitia	Linociera peglerae	Sideroxylon inerme	Strychnos madagascariensis	Ziziphus mucronata
epiphytes			nu	mber o	f times	observ	ed		
Ansellia gigantea			1						
Dermatobotrys saundersii							1		
Cyrtorchis arcuata					1		1		
Microcoelia exilis			1					1	
Mystacidium flanaganii	1			2	1				
Ficus craterostoma*			1						
F. natalensis*			1						
F. polita*									1
Microsorium punctatum**		5	3 .	1		1		1	5
Phymatodes scolopendria**†		1	3						2

^{*}Hemi-epiphyte.

After Isoglossa woodii, seedlings of Diospyros natalensis have the highest relative frequency of 10,6 per cent (Table 4). These seedlings may be encountered regularly throughout the community. Other species of the herb stratum with high frequency are Psychotria capensis, Eugenia natalitia, Teclea gerrardii and Linociera peglerae.

It furthermore becomes apparent from Table 4 that as many as 15 canopy species are represented in the herb stratum, a fact which may bear an influence on the future composition of the forest canopy.

^{**}Also present on the forest floor.

[†]Starts off as a climber, but becomes an epiphyte as the older stems die off.

Epiphytes are not rare in the Mapelana Forest, although only five true epiphytic species, of which four are orchids, were observed during the survey (Table 5). The ferns *Microsorium punctatum* and *Phymatodes scolopendria*, are found most commonly, while the three hemi-epiphytic *Ficus* species may be encountered sporadically.

The *Diospyros natalensis* community is apparently free of macrophytic plant parasites as none were observed during the survey, except one specimen of *Loranthus kraussianus* which grew on an individual of *Acacia karroo* just outside the forest.

A remarkable characteristic of the Mapelana Forest is its floristic richness. No less than 146 species were encountered during the survey as shown in the check-list. This finding supports the statements of Richards (1957), Longman and Jeník (1974) and Roger and Moll (1975) that the tropical and subtropical forests are remarkably rich compared to the temperate forests.

Quite a few species present in the Mapelana Forest are of tropical affinity and hardly occur farther south than the St Lucia area. These include *Diospyros inhacaensis*, *Inhambanella henriquesii*, *Celtis durandii* and *Pancovia golungensis*.

Conclusion

The Mapelana Forest exhibits a very luxuriant plant growth with an accompanying high density of the various strata present. This may be ascribed to particularly favourable climatic conditions for plant growth which prevail in the area.

The forest furthermore exhibits two clearly distinguishable communities due to the influence of salt-spray from the sea. The most extensive of these is the *Diospyros natalensis* community which covers the hinddune and which is not affected by the salt-spray. The other occurs on the foredune where salt-spray poisoning is intense. *Mimusops caffra* and *Strelitzia nicolai* are the most conspicuous trees on the foredune.

From the remarkable importance of *Diospyros natalensis* in all strata throughout the hinddune it could be deduced with reasonable certainty that the *Diospyros natalensis* community has reached a stable climax in which there will be no change in the dominance of this species under the prevailing environmental conditions. To the author's knowledge, the Mapelana Forest is the only locality in its range of distribution in South Africa where *Diospyros natalensis* has become the dominant of a forest community.

Both Celtis africana and Ziziphus mucronata are notably poorly represented in the lower strata. These two species may thus eventually show a decline in importance as the full-grown individuals die out and are not replaced by young plants. In contrast Linociera peglerae, Drypetes natalensis and Eugenia natalitia at present comprise important components of the lower strata and may be future subdominants of the community.

ACKNOWLEDGEMENTS

The author wishes to express his thanks to the National Herbarium of the Botanical Research Institute, Pretoria, for identifying the specimens collected in the Mapelana Forest, and to the Institute for Soils Research, Pretoria, for the analysis of the soils from the Mapelana Forest.

A special word of thanks to Mrs E. Schoonraad, Department of General Botany, University of Pretoria, for reading this article and to Prof. H. P. van der Schijff, Dean of the Faculty of Natural Science, University of Pretoria, under whose guidance the doctoral thesis, ''Die plantekologie van Richardsbaai, Natal'', was carried out by the author and of which this article constitutes part.

In conclusion the author wants to thank Mrs D. G. Roux of Bloemfontein for correcting this article grammatically.

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CHECK-LIST OF PLANT SPECIES COLLECTED OR SAMPLED DURING THE SURVEY OF THE MAPELANA FOREST

A total of 146 species, representing 117 genera and 54 families, is listed, but the check-list is not complete since the collecting was not made on an intensive scale. The families and genera are classified in systematic order according to Schelpe

(1969) and Ross (1972). Where more than one species occur in a genus, these are arranged alphabetically.

The Rubiaceae is the largest family and is represented by 10 genera and 11 species. The largest genera listed are *Ficus* and *Diospyros* with 6 and 4 species respectively.

Forty-eight of the species listed are canopy trees, 36 are subcanopy trees or shrubs, 35 are lianas and 27 species belong to the herb stratum.

PTERIDOPHYTA

POLYPODIACEAE

Phymatodes scolopendria (Burm.)
Ching
Microsorium punctatum (L.) Copel.

ASPLENIACEAE

Asplenium prionites Kunze

ANGIOSPERMAE

POACEAE.

Oplismenus hirtellus (L.) Beauv.

CYPERACEAE

Cyperus albostriatus Schrad. C. papyrus L.

COMMELINACEAE

Commelina benghalensis L. Coloetrype natalensis C.B.Cl.

LILIACEAE

Anthericum saundersiae Bak. Drimiopsis maculata Lindl. Dracaena hookeriana K. Koch Sansevieria guineensis (L.) Willd. Asparagus falcatus L. A. setaceus (Kunth) Jessop

AMARYLLIDA CEAE

Haemanthus sp. (HJTV 5506)

DIOSCOREACEAE

Dioscorea cotinifolia Kunth D. sylvatica (Kunth) Eckl.

MUSACEAE

Strelitzia nicolai Reg. & Koern.

ORCHIDACEAE

Ansellia gigantea Reichb.f.
Cyrtorchis arcuata (Lindl.) Schltr.
Mystacidium flanaganii (Bol.) Bol.
Microcoelia exilis Lindl.

ULMACEAE

Celtis africana Burm.f. C. durandii Engl. Chaetacme aristata Planch.

MORACEAE

Ficus burtt-davyi Hutch.
F. craterostoma Warb. ex Mildbr. &
Burret
F. hippopotami Gerstner

F. natalensis Hochst.

F. polita Vahl

F. sycomorus L.

URTICACEAE

Laportea peduncularis (Wedd.) Chew.

LORANTHACEAE

Loranthus kraussianus Meisn.

AMARANTHA CEAE

Pupalia atropurpurea Moq. Achyranthes sicula (L.) All.

NYCTAGINA CEAE

Commicarpus africanus (Lour.) Dandy Pisonia aculeata L.

MENISPERMACEAE.

Cissampelos torulosa E.Mey. ex Herv. Tinospora caffra (Miers) Troupin

ANN ONA CEAE

Uvaria caffra E.Mey. ex Sond. Monanthotaxis caffra (Sond.) Verdc. Annona senegalensis Pers. Monodora junodii Engl. & Diels

CAPPARACEAE

Cladostemon kirkii (Oliv.) Pax & Gilg Capparis fascicularis DC. var. zeyheri (Turcz.) Toelken Maerua racemulosa (A.DC.) Gilg & Ren

LEGUMINOSAE

Acacia karroo Hayne A. kraussiana Meisn. ex Benth. Rhynchosia caribaea (Jacq.) DC.

RUTACEAE

Teclea gerrardii Verdoorn T. natalensis (Sond.) Engl. Clausena anisata (Willd.) Hook.f. ex Benth.

MELIACEAE

Turraea floribunda Hochst. T. obtusifolia Hochst. Trichilia emetica Vahl

EUPHORBIACEAE

Heywoodia lucens Sim.
Drypetes natalensis (Harv.) Hutch.
Bridelia cathartica Bertol.f.
B. micrantha (Hochst.) Baill.
Acalypha glabrata Thunb.
Tragia rupestris Sond.
Ctenomeria capensis (Thunb.) Harv. ex
Prain

ANACARDIACEAE

Rhus natalensis Bernh. R. nebulosa Schonl.

CELASTRACEAE

Maytenus mossambicensis (Klotzsch) Blakelock var. mossambicensis M. nemorosa (Eckl. & Zeyh.) Marais M. procumbens (L.f.) Loes. Cassine aethiopica Thunb. C. papillosa (Hochst.) Kuntze Allocassine laurifolia (Harv.) N.Robson

HIPPOCRATEACEAE

Hippocratea schlechteri Loes. var. peglerae Loes.

ICACINACEAE

Apodytes dimidiata E.Mey. ex Arn.

Pyrenacantha scandens Planch. ex

Harv

SAPINDACEAE

Allophylus dregeanus (Sond.) de Wint.
A. melanocarpus (Sond.) Radlk.
A. natalensis (Sond.) de Wint.
Deinbollia oblongifolia (Sond.) Radlk.
Pancovia golungensis (Hiern) Exell &
Mendonca

MELIANTHACEAE

Bersama lucens (Hochst.) Szyszyl.

RHAMNACEAE

Ziziphus mucronata Willd. Scutia myrtina (Burm.f.) Kurz

VITACEAE

Rhoicissus tomentosa (Lam.) Wild & Drumm.
R. species (HJTV 5549)
Cissus fragilis E.Mey.
Cyphostemma cirrhosum (Thunb.)
Desc. ex Wild & Drumm.

TILIACEAE

Grewia caffra Meisn.

MALVACEAE

Hibiscus tiliaceus L.

OCHNACEAE

Ochna natalitia (Meisn.) Walp.

FLACOURTIACEAE

Dovyalis longispina (Harv.) Warb.

PASSIFLORACEAE

Adenia gummifera (Harv.) Harms

THYMELAEACEAE

Peddiea africana Harv.

LECYTHIDACEAE

Barringtonia racemosa (L.) Spreng.

RHIZOPHORACEAE

Cassipourea gerrardii (Schinz) Alston

MYRTACEAE

Eugenia gueinzii Sond. E. natalitia Sond. E. zeyheri Harv. Syzygium cordatum Hochst.

ARALIACEAE

Cussonia sphaerocephala Strey

SAPOTACEAE

Sideroxylon inerme L.
Bequaertiodendron natalense (Sond.)
Heine & J.H.Hemsl.
Mimusops caffra E.Mey. ex A.DC.
M. obovata Sond.
Manilkara discolor (Sond.) J.H.Hemsl.

Inhambanella henriquesii (Engl. & Warb.) Dubard

EBENACEAE

Euclea natalensis A.DC

E. schimperi (A.DC.) Dandy var. schim-

Diospyros inhacaensis F. White

D. natalensis (Harv.) Brenan

D. rotundifolia Hiern

D. scabrida (Harv. ex Hiern) de Wint. var. scabrida

OLEACEAE

Linociera peglerae (C.H.Wr.) Gilg & Schellenb.

Olea capensis L. subsp. macrocarpa (C.H.Wr.) Verdoorn

Jasminum streptopus E.Mey. var. strep-

LOGANIACEAE

Strychnos decussata (Pappe) Gilg S. madagascariensis Poir.

APOCYNACEAE

Carissa bispinosa (L.) Desf. ex Brenan var. acuminata (E.Mey.) L.E.Codd Voacanga thouarsii Roem. & Schult. Rauvolfia caffra Sond.

ASCLEPIADACEAE

Cynanchum ellipticum (Harv.) R.A.Dyer Secamone frutescens Decne Ceropegia grandis Bruce Tylophora anomala N.E.Br. Pergularia daemia (Forsk.) Chiov.

BORAGINACEAE

Cordia caffra Sond.

VERBENACEAE

Clerodendrum glabrum E.Mev.

LAMIACEAE

Leonotis laxifolia MacOwan

SCROPHULARIACEAE

Dermatobotrys saundersii Bol.

ACANTHACEAE

Asystasia gangetica (L.) T. Anders. Isoglossa woodii C.B.Cl.

RUBIACEAE

Mitriostigma axillare Hochst.

Xeromphis rudis (E.Mey. ex Harv.)

L.E.Codd

Gardenia thunbergia L.f.

Tricalysia lanceolata (Sond.) Burtt Davy

T. sonderiana Hiern

Kraussia floribunda Harv.

Vangueria chartacea Robyns Canthium ventosum (L.) S.Moore

Plectroniella armata (K.Schum.)

Robyns

Pavetta revoluta Hochst.

Psychotria capensis (Eckl.) Vatke

COMPOSITAE

Vernonia angulifolia DC. V. anisochaetoides Sond.

Brachylaena discolor DC.

Senecio mikanioides Otto

S. tamoides DC

STANDING CROP AND NUTRIENT STATUS OF MARION ISLAND (SUB-ANTARCTIC) VEGETATION

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ABSTRACT

The low-altitude vegetation of Marion Island (46° 54'S., 37° 45'E.) is comprised of slope, mire and fjaeldmark plant communities. The standing crop and nutrient status of these communities and a description of the soils underlying them is presented. Marion Island possesses a tundra-type biome and a comparison is made between the standing crop of the island vegetation and those of other circumpolar tundra and alpine vegetations. Slope plant communities support higher standing crops (4 480-6 645 g m⁻²) than do mire and fjaeldmark communities (2 663 and 2 742 g m⁻²) respectively. Large quantities (>1 100 g m⁻²) of dead plant material occur in the island vegetation. The above-ground standing crop (approx. 1 500 g m⁻²) in the vegetation is larger than those of most northern hemisphere tundra vegetations despite a lower cryptogamic component in the former. The below-ground standing crop of the island vegetation is lower than those of most other tundra vegetation. 1 095 kg ha⁻¹ of mineral elements (58% below-ground) accumulates in the island vegetation of which 42% is attributable to nitrogen. Because of the prominence of herbaceous plant species there is a predominance of potassium amongst the ash elements in the plant matter. Deposition of wind-whipped salt-spray on the island surface causes most island plants to contain high concentrations of magnesium and sodium.

UITTREKSEL

STAANDEOES EN MINERALE STATUS VAN DIE VEGETASIE VAN MARION-EILAND (SUB-ANTARKTIES)

Die laagliggende vegetasie van Marioneiland (46° 54′S., 37° 45′E.) bestaan uit hang, moeras en fjeldmark plantgemeenskappe. 'n Beskrywing van die staandeoes en mineraalstatus van hierdie gemeenskappe, asook 'n beskrywing van die grond word gegee. Die eiland besit 'n tundra-agtige bioom en die staandeoes van vegetasie van hierdie eiland word met ander sirkumpolêre tundra- en alpine-vegetasies vergelyk. Plantgemeenskappe van die hange het 'n hoër staandeoes (4 480–6 645 g m⁻²) as moeras (2 663 g m⁻²) en fjeldmark-(2 742 g m⁻²) gemeenskappe. Groot hoeveelhede dooie materiaal (>1 100 g m⁻²) kom in die vegetasie voor. Alhoewel daar minder Kryptogamesoorte in die vegetasie van die eiland voorkom as in tundravegetasies van die noordelike halfrond, is die begrondse staandeoes van die eilandvegetasie groter. Die ondergrondse staandeoes van die vegetasie is laer as die van ander tundravegetasies. 'n Totaal van 1 095 kg ha⁻¹ minerale elemente (58% onder-

gronds) word in die vegetasie vasgelê, waarvan 42% aan stikstof toegeskryf word. Die groot aantal kruidagtige plante veroorsaak dat die plantas 'n hoë kaliuminhoud besit. Vanweë groot hoeveelhede soutsproei wat op die eiland voorkom, is hoë konsentrasies magnesium en natrium in meeste plante bepaal.

INTRODUCTION

Marion Island (46° 54'S., 37° 45'E.) has an area of 290 km², is volcanic in origin and consists of a coastal plateau and a central mountainous region (highest peak at 1 230 m). Geographically, geologically and biologically it is a true oceanic island (Van Zinderen Bakker Sr., Winterbottom & Dyer, 1971). Being situated in the sub-Antarctic region it is subject to low temperatures, very high rainfall and a high incidence of strong winds (Table 1).

Because of the island's geologically recent origin, its relative isolation and the rigours of the terrestrial environment, the island's biota lacks in species diversity. Only thirty-five vascular plant species occur in the vegetation, of which thirteen are aliens, having been introduced by man (Huntley, 1971). Several score of bryophyte species are present, however, and dense carpets of mosses and liverworts occupy large areas of the island's surface. In addition, many species of lichen occur and algae often form thick mucilaginous mats over the wetter mire areas.

Due to the inclement weather conditions only the lowland areas (below 500 m) support closed plant communities, the mountainous interior being occupied largely by permanent ice- and snow-fields and bare, rocky peaks vegetated only by lichens and a few mosses. An overall, off-shore view of the island presents a bleak, or barren appearance owing to the absence of trees and tall shrubs in the vegetation.

The island consists of two distinctive lava types, a grey pre- and a black post-glacial type. As expected of a young volcanic island, the morphology of any particular area is strongly dependent upon its geological structure and there is a striking contrast between the glaciated areas and those which have subsequently been covered by younger lava flows. These latter areas generally form a hummocky, well-vegetated mosaic of herbfield, mire and fjaeldmark, depending upon local variation in slope, wind exposure and drainage. The smooth topography of the glaciated areas, however, offers little protection from wind erosion and consequently supports a sparser flora, mostly open fjaeldmark on the ridges with mire vegetation occupying the numerous ill-drained basins. Black lava flows form approximately 80% of the island's surface and estimates of the standing crop and nutrient status of the plant communities occupying these flows are presented in this paper. An area of approximately 1,8 ha (altitude c. 50 m) which contained typical representatives of the plant communities of the island's eastern coastal plain formed the intensive study site for both investigations.

In several aspects Marion Island possesses a tundra-type biome. Restrictively, tundra is defined as areas where the average annual temperature is below 0°C and permafrost occurs. Defined in a wider sense, however, tundra includes all areas

Dec. Nov. Oct. Sep. Aug. Climatic data for Marion Island (after Schulze, 1971). Jul. May June Apr. Mar. Feb. Jan. Frequency of days with gales

TABLE 1.

Year

rrequency or days with gales (10 years' record)	8,7	6,2		6,5 8,0	8,6	8,6 9,5	10,7	10,3	11,4	8,4	8,4	10,1	106,8
Mean monthly air temperatures, °C (12 years' record)	6,7	7,3	7,2	0,9	8,	4,0	3,6	3,2	3,3	4,3	5,1	5,8	5,1
Ms an monthly relative humidities, % (12 years' record)	81	83	83	84	83	83	84	83	83	81	81	81	83
Mean monthly precipitation, mm (15 years' record)	222	207	225	238	249	232	231	185	201	165	196	225	2 576
Mean daily total radiation reaching surface in cal. cm ⁻² day ⁻¹	495	435	316	961	142	1	113	113 181	273	416	494	508	±304
													:

where the temperature is too low or precipitation and wind too great for a natural forest vegetation to develop (Wielgolaski, 1972a). Thus oceanic moorland areas and some mountainous regions, which have somewhat higher annual temperatures, are also included. A comparison of the standing crop and nutrient status of Marion Island vegetation with that of other tundra vegetations is provided in the discussion.

TERMINOLOGY

Biomass refers to the total amount of living plant organic matter and is divided into above-ground biomass and below-ground biomass. Dead organic matter refers to dead plant material and is similarly divided into above-ground and below-ground components. The latter does not include the decomposed or humified organic constituents of the soils and peats. Above- and below-ground standing crops are the sums of the appropriate biomass and dead organic matter components, while the term total standing crop refers to the sum total of the above and below standing crops.

The magnitude of these various standing crop components are presented on a dry-weight basis and are expressed as g m^{-2} .

METHODS

1. Harvest sampling

The standing crop estimates reported in Table 4 reflect the average maximum standing crops attained by the plant communities in the study site during the 1971–2 and 1973–4 growing seasons.

In each plant community the average aerial cover of the overall vegetation and of each species was found using a series of 50×50 cm quadrats. Quadrat samples for harvest were taken separately for each species from areas within the plant community containing between $90{\text -}100\%$ aerial cover of the particular species. The living and dead plant material was clipped to soil-level and all litter also collected. The harvested material was sorted into categories of plant organs (flowers, stems, leaves, sporulating fronds, etc.) and oven-dried at 105°C to constant weight. The oven-dry weights of these organs were readjusted to the average percentage cover of the particular species within the community. The dried harvested material was kept for chemical analysis.

The size and number of sampling unit replicates used in the harvesting depended upon that needed to obtain a reliable (<25% coefficient of variation) estimate of the above-ground standing crop of the particular species. For most species 4–6, 0,1 m² sampling units were used. The extremely uniform structure of pure stands of *Blechnum penna-marina* (Poir) Kuhn and of cushions of *Azorella selago* Hook.f. enabled similarly reliable estimates of the aerial standing crops of these two species to be derived from 4–6, 50 cm² circular sampling units.

Below-ground standing crop was sampled at each clipped site using a 50 cm²

core borer which removed a plug of earth with roots and rhizomes to a depth of 50 cm. These were washed free of soil and organic debris, sorted into species and the visibly dead material separated from the living material. The separate components were oven-dried, weighed, and the oven-dry weights readjusted in the same manner as those of the aerial plant material. Because of the difficulties encountered in distinguishing the living from the dead underground material of some species, these two components are not reported separately in this account but rather a composite figure (below-ground standing crop) is presented.

The relative areas occupied by each community on the surface of the intensive study site are not representative of their proportions in the black lava regions of the island's eastern coastal plain as a whole. In order to provide an estimation of the overall vegetation standing crop of these regions, an assessment of the true extent of each community within the larger area had to be made. Accordingly, diagonal traverses of a 10 km² area on the eastern coastal plain of the island were marched on fixed compass bearings and the number of footfalls, or footsteps in each plant community encountered on the marches was recorded, i.e. each footstep was regarded as a point. Points were 75 cm apart and this distance was kept constant by a piece of string tied between the walker's feet. This modified step-point method proved to be a rapid means of assessing the relative areas occupied by the different plant communities.

2. Chemical analyses: plant material

Ash elements: 1 g of the harvested plant material was ashed at 450°C for 1½ hours in a muffle furnace, the ash dissolved in concentrated HNO3 and the acid evaporated off. The ash was replaced in the furnace for 20 minutes at the same temperature and the resultant residue taken up in hot, dilute HNO3. The concentrations of calcium, magnesium, sodium, potassium and iron in the ash extract were determined by atomic absorption spectrophotometry and the amount of phosphorus by the method of Kitson and Mellon (1944).

Nitrogen was measured according to the method used in the determination of the total nitrogen content of soils. Although losses of N from plant tissue dried at 105°C have been reported in the literature, no significant differences were found in the nitrogen contents of replicate samples of most Marion Island plant species dried at 60°C, 80°C or 105°C. Tissue inherently high in nitrogen, however, exhibited slightly lower measured nitrogen values when dried at 60°C rather than 105°C, probably due to enhanced enzymatic breakdown of tissue proteins with subsequent volatilization of the newly released N fractions during the slower killing of the tissue at the lower temperature. Green tissue dried at 105°C retained its colour during the drying period and reached constant weight in 12–48 hours against 36–72 hours needed for similar tissue at 60°C. The latter never retained its green colour during the drying period. High humidity of the laboratory air on the

island was almost certainly responsible for the retarded drying of the plant tissue at 60°C.

3. Chemical analyses: soils

Inorganic nitrogen was determined on fresh, undried soil samples. All other analytical procedures were performed on air-dried, sieved (2 mm) soil samples excepting for organic carbon determinations which were made on ground (0,2 mm) samples. Results of the determinations are expressed per unit oven-dry weight of the soils.

Total nitrogen content was determined according to the regular macro-Kjeldahl method of Bremner (1965a) excepting that a steam distillation method was employed for the determination of ammonia in the digest. Inorganic nitrogen: the MgO-Devarda Alloy steam distillation method whereby KCl extracts of fresh soils were analysed for ammonium and nitrate-nitrogen (Bremner, 1965b), was used. Organic carbon was measured by the Walkley-Black method (Allison, 1965), modified slightly in that a 2N dichromate solution was employed. Organic carbon values reported in Table 3 are uncorrected for soil chloride content. Total phosphorus was determined by the ignition method of Legg and Black (1955) except that the ignited soils were taken up in 10 N HNO3 rather than in conc. HCl. The concentrations of P in the extract were determined according to the method of Kitson and Mellon (1944).

Soil cation exchange capacity was determined by saturating the soils' adsorption complex with Ca²⁺ by equilibrating 5 g soil samples with 0,1 M CaCl₂. After removal of the free calcium ions in the soil solution with rinses of isopropanol the saturating Ca²⁺ ions were displaced using 1 N NH₄ NO₃ in 60% ethanol solution and the concentration of these ions in the leachate measured by atomic absorption spectrophotometry.

Total exchangeable cations: A 5 g soil sample was washed by filtering through small portions of 60% ethanol and the adsorbed cations then displaced using a 1 N NH₄Cl in 60% ethanol solution. The concentration of cations in the leachate was measured by atomic absorption spectrophotometry.

Soil pH was measured in a soil suspension of 1 part soil: 2 parts 0,01 M CaCl₂ solution (W: W) and soil water content determined by drying fresh samples of soil at 105°C to constant weight.

DISCUSSION AND RESULTS

1. Description of the vegetation and soils

The younger black lava areas of the island coastal plain are typified morphologically by being extremely hummocky and, except for the exposed rocky ridges and plateaux, well vegetated (Fig. 1). Several distinct plant communities occur within the black lava areas. These may be grouped into three categories, viz. (i) vegetation of the slope complex, (ii) mire vegetation, and (iii) vegetation of the exposed rocky plateaux, or fjaeldmark.

(a) The slope complex

Five plant communities occupy the numerous slopes of the hummocks and ridges of the island's low-altitude black lava areas. A summary of their floristic composition is provided in Table 2 while a more detailed description of their nature and distribution may be found in Huntley (1971).



Fig. 1.

Overall view of the hummocky, low-lying north-eastern coastal plain of Marion Island. Distance from photographer to rock in sea is approx. 7½ km.

The soils under the slope plant communities are remarkably similar regarding their profile characteristics. Slope soils overlie porous loose-rock and scoria deposits and, except for those occurring directly in drainage lines, are consequently well drained. The chemical status of the slope soils differs according to the vegetation cover, however, and chemical data for the upper horizons of these soils is presented in Table 3.

(i) Blechnum penna-marina fernbrake community.

The dominant cover of slopes protected from the icy southern and south-western winds is that of a thick continuous carpet of the fern *Blechnum penna-marina* which may occupy several hundred square metres of such leeward slopes (Fig. 2). Cushions of *Azorella selago* and tussocks of the grass *Poa cookii* Hook.f. are frequent in the otherwise uniform fern carpet and, where rocky outcrops occur, the rosaceous shrub *Acaena magellanica* (Lam.) Vahl. occurs. Other vascular plant

Percentage aerial cover values of component species in the plant communities occurring on the black lava flows of the Marion Island eastern coastal plain. TABLE 2.

Total

106 97 183 108 189

26

53

Plant community	B. penna- marina	Poa cookii	A. selago	A. selago A. (1) mag- A. (2) mag- ellanica ellanica	4. ⁽¹⁾ mag- A. ⁽²⁾ mag- ellanica ellanica	Bryo- phytes	Algal mats	Other
SLOPE COMPLEX								
B. penna-marina fernbrake	79	6	15	3	tr	Ħ	nil	Ħ
Open, scrub community	42	œ	31	15	_	liu	liu	nil
A. (1) magellanica drainage line	24	_	3	7.5	ni.	80	nil	Ц
P. cookii, A. selago crest	=	57	36	2	2	ΙL	liu	liu
P. cookii tussock grassland	=	37	=	43	liu	85	liu	2
MIRE COMPLEX $A^{(2)}$ magellanica mire	ıja	ī	F	liu	49	75–90	0.5-1	1230
FJAELDMARK A. selago fjaeldmark	6	lia	27	lin	91	-	lin	ŢŢ
(1) Acaena magellanica (2) Agrostis magellanica (3) Including Univing Albi (1807) Trucus solvenisidae (107)	one doe one on	. sopioinory	(10)					

⁽³⁾ Including Uncinia dikei (8%), Juncus scheuchzerioides (4%). tr = trace, less than 0,5%.

Chemical status of the horizons containing living roots in the soils under Marion Island plant communities TABLE 3.

cm Plant community N Depth	Z	cm Depth	Ηd	% Water	Ca	% satur Mg	% saturation of C.E.C. Mg Na K	f C.E.C. K	Total	% Org.–C	% Total–N	% Total–P	mg/100 g soil NH4-N NO3-N	mg/100 g soil IH4-N NO3-N
SLOPE COMPLEX B. penna-marina fembrake	∞	0-18	4,3	715±67,0	21±5,2	40±2,2	4±0,8	7±2,1	72±5,4	43,8±1,33	715±67.0 21±5,2 40±2,2 4±0,8 7±2,1 72±5,4 43,8±1,33 2,18±0,161 0,74±0,195 tr.—1,6 0,0-tr.	0,74±0,195	tr1,6	0,0-tr.
Open scrub community	4	0-10	N.D.	325±45,9	13±2,9	14±2,1	4±0,9	1±0,5	31±5,4	12,7±3,16	325±45,9 13±2,9 14±2,1 4±0,9 1±0,5 31±5,4 12,7±3,16 1,24±0,310 0,52±0,093	0,52±0,093	tr0,9	0,0–tr.
 Magellanica drainage line 	9	0-45	4,2-4,7	$0-45 4,2-4,7 1 002\pm275,0 26\pm1,1 32\pm9,0 4\pm1,9 2\pm1,0 65\pm10,8 42,9\pm10,66 2,50\pm0,442 0,66\pm0,224 2,10,10 $	26±1,1	32±9,0	4±149	2±1,0	65±10,8	42,9±10,66	2,50±0,442	0,66±0,224	tr2,9	0,0-tr.
Poa cookii, A. selago crest	4	0-17	4,3-4,4	$0-17 \ \ 4,3-4,4 \ \ \ 450\pm328,8 \ \ \ 11\pm4,5 \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \$	11±4,5	14±6,8	5±2,3	2±2,3	31±15,8	23,9±16,20	1,63±0,733	0,56±0,480	tr1,7	0,0–tr.
Poa cookii tus- sock grassland	∞	0-50	0-50 4,0-4,1	360±23,2	14±1,2	13±3,0	5±2,2	1±0,5	34±4,1	25,0±4,73	$360 \pm 23.2 14 \pm 1.2 13 \pm 3.0 5 \pm 2.2 1 \pm 0.5 34 \pm 4.1 25.0 \pm 4.73 1.66 \pm 0.298 1.55 \pm 0.456 0.9 - 8.4 0.0 - 1.0 1.00 \pm 0.0 + 1.00 \pm 0.0 + 1.00 \pm 0.0 + 1.00 \pm 0.0 $	1,55±0,456	0,9–8,4	0,0-1,0
MIRE COMPLEX Agrostis magella- nica mire	10	10 0-20	4,2	1 667±199,1 5±1,5 13±0,5 5±0,7 3±1,0 26±1,5 48,1±4,93 2,34±0,420 0,60±0,491	5±1,5	13±0,5	5±0,7	3±1,0	26±1,5	48,1±4,93	2,34±0,420	0,60±0,491	2,4-6,5 0,0-0,7	0,0-0,7
FJAELDMARK <i>A. selago</i> fjaeldmark	4	4 0-10		N.D. 217±168,4 3±2,1 9±3,4 3±1,9 2±3,3 17±5,9	3±2,1	9±3,4	3±1,9	2±3,3	17±5,9	6,0	0,73	0,42	0,0-0,5 0,0-tr.	0,0-tr.

N = number of determinations.

Values expressed as ranges or as means \pm standard deviations. N.D. = not determined. It. = trace (< 0,5 mg/100 g soil).

species account for less than 1% of the vegetation cover (and standing crop) of this plant community which, following Huntley (1971), is termed *fernbrake* vegetation. The moss *Rhacomitrium lanuginosum* (Hedw.) Brid. and the liverwort *Plagiochila crozetensis* Kaal., the latter usually associated with *A. selago* cushions, also occur but the non-vascular component commonly accounts for less than 0,5% of the total vegetation cover of fernbrake communities.



FIG. 2.

Blechnum penna-marina fernbrake community on an east-facing slope. A narrow drainage line connecting two mire areas and dominated by Acaena magellanica is prominent. Height of slope approx. 20 m.

(ii) Open scrub community.

Slope areas offering less protection from the wind, or which are occupied by a large number of rocky outcrops breaking the soil cover, support a stunted *Blechnum penna-marina* vegetation cover in which there is an increased importance of *Azorella selago* and *Acaena magellanica* (Fig. 3). The aerial cover of the vegetation of these areas is indicated in Table 2 as being almost 100%. This is due to the increased *A. magellanica* canopy over the *Blechnum* fronds and to a greater expanse of *A. selago* cushions, on which the other component species often occur epiphytically. Basal vegetation cover of these areas is much lower than that of fernbrake areas and the vegetation has an open, scrubby appearance. Although the term *scrub* is most usually associated with arboreal vegetation, it has been used in describing low-growing, sub-climax vegetation covers (Ashby, 1969) and in this

account the term scrub community is used in referring to the open vegetation of the exposed or rocky-slope areas.

The soils under fernbrake and scrub communities are similar in profile characteristics excepting that the latter soils are somewhat shallower. A fibrous mat of *B. penna-marina* rhizomes, fronds and litter merges with a black or dark-brown



Open scrub community of Blechnum penna-marina, Azorella selago, Poa cookii and Acaena magellanica. Distance of A. selago cushions in foreground to large

rock at upper right is approx. 10 m.

humic A horizon, the upper regions of which contain dead plant remains and live roots. A well-developed B horizon occurs beneath this A horizon, changing from dark-brown through yellow-brown to a red-orange colour with increasing depth. This latter colour represents the zone of sesquioxide enrichment and an iron pan is most often present, usually immediately above the parent rock.

The upper soil horizons under fernbrake communities are more organic and possess higher water and total nitrogen contents than do those under scrub communities (Table 3). The lower water retention of the scrub soils allows for more intensive leaching of nutrients, possibly explaining the lower percentage base saturation of these soils.

All non-biotically influenced slope soils possess low contents of inorganic nitrogen, predominantly in the ammonium form. Negligible concentrations of nitrate nitrogen occur, as might be expected under the low pH-low temperature soil régime.

(iii) Wet, Acaena magellanica-dominated drainage line community.

Depressions and drainage lines in the slope areas are invariably occupied by a dense canopy of *Acaena magellanica* interspersed with long etiolated fronds of *Blechnum penna-marina* and understoreyed by a luxuriant growth of the moss *Brachythecium rutabulum* (Hedw.) B.S.G. (Figures 2 + 4). The vegetation of these drainage lines and depressions is equivalent to the *Acaena decumbens* (= *A. magellanica*, Walton, pers. comm.) – *Tortula robusta* Hook. et Grev. communities of sheltered depressions attracting run-off water in slope areas on South Georgia (Walton, 1973). Although rapid flow of water occurs through the soils under Marion Island drainage line communities, the deeper layers of the humusrich, clayey B horizon of these soils are often anaerobic. The soils are very wet and the water-table seldom more than a few cm below the surface.

The percentage base saturation of drainage line soils is less than that of surrounding soils under fernbrake, largely because of lower contents of magnesium in the former (Table 3). This may be due to the ease with which magnesium is leached from colloidal adsorption surfaces. The increased importance of calcium in the cation suite of drainage line soils is reflected by increases in the content of this element in the leaves of *Acaena magellanica* plants growing in these soils (see section 3a).



Poa cookii – Azorella selago community on crest of slope. Wet depression dominated by Acaena magellanica prominent in foreground. Fjaeldmark at right and mire vegetation in background at left. Width of crest community approx. 5 m at widest point.

(iv) Poa cookii - Azorella selago slope-crest community.

On the exposed crests of slopes supporting a fernbrake community a narrow bank of *P. cookii* understoried by large cushions of *A. selago* often occurs (Fig. 4). Both these species are tolerant of cold air and cold soil (Huntley, 1971) and this may be the reason for their association in this distinctive band, which is seldom more than 3–5 m wide, on the exposed crests of the slopes.

The soil profiles under the *crest* communities are essentially similar to those under fernbrake excepting that the lighter-coloured A horizon of crest soils is less humic and that larger quantities of scoriae occur in the deeper soil horizons. The content of organic carbon, total nitrogen, total phosphorus and adsorbed cations is lower in these soils than in those under fernbrake (Table 3).



Fig. 5.

Poa cookii tussock grassland on inland, east-facing slope. Dense Acaena magell-anica cover is obscured by the long leaves of the grass. Height of slope approx. 20 m.

(v) Poa cookii tussock grassland.

In many well-drained, protected slope areas the *Blechnum penna-marina* carpet is replaced by a dense plant cover comprising *Acaena magellanica* codominant with luxuriant swards of *P. cookii* (Figures 5 + 6). A dense understorey of *Brachythecium rutabulum* occurs and *Azorella selago* and *B. penna-marina* are common throughout this community, which has been termed *inland tussock grassland* by Huntley (1971) and which is invariably undermined by numerous

burrows of small petrel and prion species. The high inorganic nitrogen contents of the soils under inland tussock grassland communities (Table 3) evidences the influence of the birds on the nutrient status of these soils. In relation to their relatively low organic carbon values, the total phosphorus content of tussock grassland soils is also high, possibly indicating enrichment in inorganic phosphorus by the bird guano. This is substantiated by the effect which these birds have on the nutrient status of the plants growing in the inland tussock grassland communities (Smith, 1976).



Close-up of *Poa cookii* tussock grassland. *Acaena magellanica* cover visible in shadows of grass tussocks. Height of tussocks approx. 60 cm.

(b) The mire complex

The topography formed by the younger lavas as well as the extremely porous and *blocky* structure of these lavas is of such a nature that very few stream courses exist in areas covered by them. Considering the high rainfall, considerable amounts of water must reach the sea via underground drainage. A characteristic feature of the hummocky topography is, in fact, the numerous small bogs between the humps in which subsurface drainage from the surrounding slopes is ponded.

In many such areas the bogs have been succeeded by soligenous mires (Fig. 7). The dominant vascular plant cover of these mires is an open canopy of the grass *Agrostis magellanica* Lam. under which numerous individuals of *Uncinia dikei* Nelmes and *Juncus scheuchzerioides* Gaud. usually occur (Table 2). Several

bryophyte species often form a dense carpet under the A. magellanica canopy; the most common of these are Drepanocladus uncinatus (Hedw.) Wernst., Rhacomitrium languginosum and Plagiochila crozetensis. In extremely wet regions a dense carpet of Blepharidophyllum densifolium (Hook.) Angstr. Arnell develops.

The water-table is almost continuously at the surface within the mire areas. Peat formed in these areas is deep and amorphous and mineral horizons seldom occur within the profile.



Fig. 7.

Agrostis magellanica mire community with slope complex in background. Distance to near edge of lava lakelet approx. 60 m.

The ammonium nitrogen status of mire peat is fairly high in comparison with that of the slope soils (Table 3), although not as high as those of many other peaty soils where values of 40–60 mg 100 g soil⁻¹ have been reported (Harmsen and Kolenbrander, 1965). These relatively high values for ammonium nitrogen in the island peat may be due to the breakdown of labile organic substances during the distillation procedure, despite precautions employed against this (filtration of the soil extract, use of MgO and short distillation times). It is of interest, however, that all peat samples exhibiting the higher values in the range of ammonium nitrogen contents reported in Table 3 occurred under a thick gelatinous algal mat containing *Nostoc commune* Vaucher (although the presence of such a mat did not always imply a high ammonium nitrogen content). Croome (1973) has shown that *N. commune* fixes significant quantities of atmospheric nitrogen in the island

mires and the data in Table 3 indicate that this fixation serves to enrich these mires in reduced nitrogen.

(c) The exposed rocky plateaux: fjaeldmark communities

Exposure to wind limits the growth of most plant species on the rocky plateaux. Azorella selago, Agrostis magellanica and a few scattered, stunted individuals of Blechnum penna-marina form the vegetation cover of these areas (Table 2). In areas completely exposed to the wind, the total plant cover seldom exceeds 5%. These are the true fjaeldmark, or wind desert, communities and occur mainly above the 200 m contour (Huntley, 1971). On the rocky plateaux of lower-lying areas, however, the cushions of A. selago are large and very numerous, supporting many epiphytic individuals of A. magellanica (Figures 4+8). The percentage aerial cover of the vegetation in such areas is between 50% and 60% and basal cover may be as high as 50%.



Fig. 8

Rocky, exposed plateaux supporting a relatively well-vegetated fjaeldmark community typical of the low-lying island regions and dominated by *Azorella selago* and *Agrostis magellanica*, the latter mostly epiphytic on cushions of the former. Distance to rocky outcrops in background approx. 15 m.

Soils developed under fjaeldmark vegetation are skeletal, gravelly loams of a shallow nature. Where plants are growing at the immediate surface the amount of soil organic matter in the top few cm may be high owing to the slow breakdown of the plant remains in the low temperatures prevalent in fjaeldmark areas. Fjaeldmark soils are, however, generally much less organic than are those of the mire

TABLE 4.

		1010	10 5	contains of triangle island plant communities	ant collin	namnes.			
			stano	standing crop component (g m-2)	nent (g m	-2)			
			Abo	Above-ground		Below-	Total	Surf.	S.C. ii
Plant community	Bion	nass		Dead	Total	punoa	Stand	Area	Average
	Vasc.	Vasc. Cryp.	Total	O.M.	S.C.	S.C.	Crop	Occup.*	Hectare*
SLOPE COMPLEX									
Fernbrake community	568±79	Ħ	568	568 1 557 ± 322	2 125	3.984 ± 684	6 109	18.0	10 996
Open scrub community	438 ± 63	tr	438	1 580 ± 208	2 018	2 462 ± 441	4 480	21.6	077 01
Acaena drainage line	727 ± 92	224 ± 94	951	528 ± 107	1 479	3607 ± 572	5 086	0.3	153
P. cookii, A. selago crest	804 ± 117	tr	804	3654 ± 1086	4 458	2001 ± 227	6 459	1,0	646
P. cookii tussock grassland	778 ± 134	230 ± 49	1 008	1 008 1 649 ± 225	2 657	3.988 ± 898	6 645	9,0	399

*percentage **kg ha⁻¹

096 6

37.4

2 663

 2024 ± 421

639

 303 ± 69

336

 219 ± 82

 117 ± 29

Agrostis magellanica mire

MIRE COMPLEX

5 731

20,9

2 742

 963 ± 224

1 779

ţ

 238 ± 36

Azorella selago fjaeldmark

FJAELDMARK

TABLE 5. Standing crops of sub-Antarctic and other tundra-type vegetations.

Tundra-type Location and Vegetation			nding Cro		ent (g m ⁻²)		T 1
Location and vegetation	В	iomass	we-ground	Dead	Total	Below- ground	Total in
	Vasc.	Cryp.	Total	O.M.	Above	Total	S.C.
Sub-Antacrtic		- 71					U.C.
Marion Island (1972, 1974)							
Mosaic of slope, mire and fjaeldmark							
vegetation	306	84	390	1 105	1 495	2 262	3 757
Marion Island (1969) ¹			=				
Fernbrake community			799				
Tussock grassland			449				
Agrostis mire Macquarie Island ² (54° 30′ S.)			329				
Pleurophyllum hookeri herbfield			760				
Poa foliosa tussock grassland	920		920*	3 300*	4 220*	8 400*	12 620#
South Georgia (54° 16′ S.)	920		720	3 300	4 220	0 400	12 020
Acaena magellanica wet depression ³	1 117	221	1 338	519	1 857	7 536	9 393
Festuca erecta grassland ⁴	424	170	594	1 654	2 248	1 682	3 930
Sub-Arctic and Low-Arctic							
Koryak National Territory, U.S.S.R.5							
Mosaic tundra of sedges, mosses, lichens							
and shrubs	218	261	479	521	1 000	2 307	3 307
Hillocky tundra of sedges, mosses, lichens							
and shrubs	250	241	491	410	901	2 387	3 288
Vorkuta Region, U.S.S.R.6	100	210	507	2//	072	(22(7 000
"Typical" tundra of low shrub, mosses	188	319	507	366	873	6 226	7 099
Woody sub-Arctic shrub-dwarf shrub tundra	817	1 345	2 162	24	2 186	15 016	17 202
Abisco (68° 15′ N.) ⁷	01/	1 343	2 102	24	2 100	13 010	17 40-
Calamagrostis purpurea grassland			234				
Calamagrostis purpurea grassland max.			458				
Sedge swamp			242				
Sedge swamp max.			373				
Arctic							
Devon Island Truelove Lowland							
(75° 40′ N.)8							
Sedge meadows, beach meadows and							
rock outcrops	79		79*	143*	222*	1 090*	1 312
Bolshoy Lyakovskiy Island, U.S.S.R. ⁵							
Hummocky tundra of sedges, grasses,							1.07/
shrubs and mosses	71	115	186	69	255	821	1 076 532
Polygonal moss and forb tundra	49	70	119	61	180	352	334
Barrow, Alaska (71°20′ N.)9							
Predominantly graminoid-species vege-					112-	1 520-	1 778
tation					266	2 185	2 438

* excluding cryptogamic component.

1. Huntley (1972a).

Jenkin and Ashton (1970).
 Walton (1973).

4. Greene, Walton and Callaghan (1973).

5. Rodin and Bazilevich (1967).6. Bliss (1973).

7. Pearsall and Newbould (1957).

8. Calculated from the data of Bliss and Kerik (1973), Muc (1973) and Svoboda (1973).

9. Dennis and Johnson (1970).

Alpine							
Mount Washington ¹⁰							
Carex bigelowii meadow			203– 208				
Rush-dwarf heath meadow			81-				
			109				
Mts Wyoming 10							
Carex scapulosum-Deschampsia caespi-							
tosa meadow			112				
Koryak National Territory, U.S.S.R. ⁵							
Alpine shrub tundra	80	25	105	54	159	1 244	1 403
Non-tundra type							
Osage, U.S.A. ¹¹							
Mixed tall-grass species prairie	274		274	230	504	1 184	1 688

^{10.} Bliss (1962).

and slope complexes (Table 3). The soils are also very poor in base content, due possibly to rapid percolation of incoming rainfall through these soils because of their low water-retention capacity.

2. Standing crops of the plant communities

The standing crop values of the various plant communities at the time of maximum above-ground biomass and the contribution of these communities, in relation to their proportionate representation, to the average standing crop of one hectare of the black lava areas of the island's eastern coastal plain are presented in Table 4. In Table 5 a comparison of this average standing crop with those of other circumpolar tundra and alpine vegetations is provided.

(a) The slope complex

The plant communities of the slope complex support far higher standing crops of plant matter than do those of the mire and fjaeldmark areas (Table 4). This is due to the higher above-ground biomass and below-ground standing crop of the slope communities and is in accordance with the results of other studies on hummocky and hillocky tundra areas (Rodin and Bazilevich, 1967).

The estimate of 568 g m⁻² for the above-ground biomass of Marion Island fembrake vegetation is substantially lower than the corresponding value (799 g m⁻², Table 5) reported by Huntley (1972a) for April 1969. This earlier estimate was based upon a fernbrake stand possessing a high (95%) cover of *Blechnum penna-marina* with *Azorella selago* contributing only 5% towards the total aerial vegetation cover. Although such well-developed stands do occur on slopes offering complete protection from southern winds, the average *B. penna-marina* cover of typical fernbrake areas is usually much lower and *A. selago*, a species exhibiting a low above-ground biomass, is of greater importance in such areas.

^{11.} Sims and Singh (1971).

Expectedly, the open, stunted plant growth of the exposed scrub slopes causes these areas to exhibit the lowest above-ground biomass and overall standing crop of all the communities of the slope complex. An examination of the floristic composition of the vegetation of these scrub areas (Table 2) demonstrates the importance of *A. selago* in the standing crop of this vegetation. The cushion habit of this species allows negligible dissemination of the produced leaf and stem material once this has died even though the cushions are commonly found in areas subjected to long periods of gale-force winds. Considering that some cushions on Marion Island are estimated to be over 100 years old (Huntley, 1972b), large quantities of dead material can accumulate and this contributes substantially to the overall vegetation standing crop. Huntley (*l.c.*) considers that *A. selago* has the highest standing crop of all the vascular plants on the island. *Azorella* cushions occupy 31% of the scrub areas and without the dead material contained in them these areas would support a very much lower standing crop than is indicated in Table 4.

Previous workers have shown that extremely large amounts of dead plant material accumulate in the swards and tussocks of sub-Antarctic and Antarctic grasslands. The graph presented by Jenkin and Ashton (1970) indicates that approximately 80% of the above-ground standing crop of *Poa foliosa* Hook.f. grassland on Macquarie Island consists of dead *P. foliosa* while Greene, Walton and Callaghan (1973) found that 71% of the above-ground standing crop of a *Festuca erecta* D'Urv. grassland community on South Georgia was accounted for by dead material, predominantly that of *F. erecta*, despite the fact that living material of this species contributed only 8% towards the total standing crop of the vegetation. Data reported by Edwards (1973) indicate that dead plant material constitutes between 40% and 90% of the above-ground standing crop of a closed *Deschampsia antarctica* Desv. sward on Signy Island (Maritime Antarctic).

The current study on Marion Island supports these previous observations and large amounts of dead (and living) plant matter accumulate in the perennial tussocks of the grass *Poa cookii*. The dominance of this species, along with that of *A. selago*, in the narrow bands of vegetation on the crests of slopes causes these areas to support by far the highest above-ground standing crop (4 458 g m⁻²) of all the island plant communities, despite the absence of a significant bryophyte stratum beneath the *Poa* canopy. This value is similar to that reported by Jenkin and Ashton (1970) of 4 220 g m⁻² for the above-ground standing crop of Macquarie Island tussock grasslands (Table 5), considering that the bryophyte component was not included in their estimate. Because of the low below-ground standing crop, however, the total standing crop of the Marion Island slope-crest communities is approximately half that of the Macquarie Island tussock grasslands.

Many large perennial roots and rhizomes are developed by Acaena magellanica plants and communities in which this species is an important constituent exhibit

high below-ground standing-crop values (Table 4). This is in accordance with similar observations on *A. magellanica*-dominated communities on South Georgia (Walton, 1973; Greene, *et al.*, 1973). The luxuriant growth of *Brachythecium rutabulum* which occurs under the *Acaena* canopy on Marion Island also adds substantially to the overall vegetation standing crop in these areas.

The above-ground vascular biomass of wet depressions dominated by A. magellanica on South Georgia (Table 5) is approximately 50% greater than that of the depression and drainage line communities on Marion Island. This reflects the lower percentage cover of A. magellanica in the Marion Island communities. Blechnum penna-marina, a species possessing no above-ground perennial tissue, constitutes roughly a quarter of the vegetation cover in these communities, in contrast to the complete dominance of Acaena in the South Georgian communities (Walton; l.c.). The underground standing crop of the South Georgian communities is twice that of the corresponding communities on Marion Island. The total standing crop in the former is therefore extremely high, ranking with that of many sub-Arctic shrub tundras and with that of Macquarie Island tussock grassland.

The importance of the three species, *Poa cookii*, *Azorella selago* and *Acaena magellanica* in the tussock grassland of the slope complex causes this community to exhibit the highest total standing crop of all Marion Island plant communities. The above-ground biomass of tussock grassland (1 008 g m⁻²) is more than double that reported by Huntley (1972a) and is considerably higher than that of a similar, well-developed *Festuca erecta-Acaena magellanica* community on South Georgia (Greene, *et al.*, 1973).

The floristic composition of tussock grasslands on Marion Island varies considerably, although P. cookii always retains its prominence. Huntley's estimate is based upon a virtually pure stand of 30 cm high tussocks of this grass, which are typical of steeply sloping, well-drained, sea-facing slopes of the shore region and which are usually heavily influenced by animals. In these areas the ground between the tussocks is only sparsely vegetated by small coprophilous species such as Callitriche antarctica Engelm. ex Hegelmeyer. In contrast, inland stands of P. cookii tussock grassland are codominated by Acaena magellanica which occurs in abundance between the grass tussocks (Fig. 6). A well-developed bryophyte stratum also occurs under this Acaena canopy. Although numerous burrows of small petrel and prion species undermine these inland areas, damage due to trampling is minimal and no bare ground occurs between the grass tussocks. The greater vegetation cover of the inland tussock grassland communities, added to the fact that the mature grass tussocks are 40-50 cm high, accounts for the disparity between the aerial biomass value for Marion Island tussock grassland reported by Huntley (1972a) and that of the current investigation.

The vascular above-ground biomass of the taller (1 1,5 m) *Poa foliosa* tussocks on Macquarie Island (Table 5) is substantially higher than that of the smaller *P. cookii* tussocks on Marion Island but it is noteworthy that, similar to the Marion

Island tussock grasslands, those of Macquarie Island do not rely solely upon tussocks of *Poa* for their high aerial biomass values. *Stilbocarpa polaris* A. Grey is codominant with the grass in many of these areas (Taylor, 1955; Jenkin and Ashton, 1970) and the large leaves of this plant add substantially to the aerial biomass of the vegetation.

(b) The mire complex

The occurrence of only small amounts of living and dead vascular plant material in mire areas causes the vegetation of these areas to exhibit a low total standing crop compared with those of the slope communities (Table 4). The standing crop estimate included in the table for this vegetation does not include the algal mats which occur on the surfaces of the wetter mire areas. Dry weights of up to 500 g m⁻² have been reported for these mats (Croome, 1973) but as they typically occupy less than 1% of the total mire surface (Table 2 and Croome, *l.c.*) they do not contribute significantly to the overall standing crop of the mire vegetation.

The above-ground biomass value of the mire vegetation agrees closely with that presented by Huntley (1972a) (Table 5) and is similar to that of graminoid-dominated swamps and clearings in the sub-Arctic of Swedish Lappland (Pearsall and Newbould, 1957) but is higher than that of alpine meadows (Bliss, 1962) due to the importance of bryophytes in the island mires. This importance is further demonstrated by the fact that the mires, although occupied by an open, low-growing vascular plant cover, support a higher biomass and total standing crop of vegetation than does a prairie grassland consisting of mixed, tall-grass species which exhibited the highest maximum above-ground biomass and standing crop (Table 5) of all those investigated in the United States IBP Grassland Biome Study (Sims and Singh, 1971). Huntley (1972a) states that a mire community on Marion Island, with only 35% aerial vascular plant cover and 15 cm in height, has a higher aerial biomass than that of many tropical grasslands.

(c) The fjaeldmark vegetation

The lowest above-ground biomass (and below-ground standing crop) values of all the plant communities are exhibited by the fjaeldmark vegetation (Table 4). Total standing crops of mire and fjaeldmark communities are, however, approximately equal because of large amounts of dead plant material in the *Azorella selago* cushions of the latter. True fjaeldmark, or wind desert, communities support much lower amounts of plant organic matter due to increased environmental adversity and decreased plant cover. As indicated previously, relatively well-vegetated fjaeldmark vegetation, rather than wind desert, is more representative of the rocky plateaux and ridges of the low-lying island areas.

(d) Comparison of the standing crop of Marion Island vegetation with those of northern circumpolar tundra and alpine vegetations (Table 5)

Fernbrake, open scrub, fjaeldmark and mire communities occupy 98% of the black lava flows of the island's eastern coastal plain and account for approxima-

tely 97% of the total vegetation standing crop of this area. Thus, despite their high standing crops, the grassland and drainage line communities do not contribute markedly to the overall vegetation.

The above-ground biomass of vascular plants in the island vegetation (306 g m⁻²) is approximately one third greater than those of mosaic and hillocky tundra areas consisting of sedges, mosses, lichens and dwarf shrubs of the U.S.S.R. low Arctic and sub-Arctic and is four times greater than that of the Devon Island (Canadian Northwestern Territories) Truelove Lowland. The average aerial biomasses of sub-Arctic grassland and sedge-swamp communities in Swedish Lappland are also lower than that of the island vegetation. Compared with these northern tundras, however, a low (84 g m⁻²) biomass of cryptogams occurs in the island vegetation, reflecting the relative importance in this vegetation of plant communities which do not support a significant bryophyte growth. Because of this low cryptogam component the total above-ground biomass of the island vegetation is lower than those of the sub-Arctic and low-Arctic areas.

Large amounts (over 1 100 g m⁻²) of above-ground dead plant material accumulate in the island vegetation, thus the above-ground standing crop (approx. 1 500 g m⁻²) is substantially higher than those of comparable low-growing sub-Arctic and low-Arctic tundra vegetations (870–1 000 g m⁻²). Extensive sub-Arctic areas in Canada and the U.S.S.R. are occupied by a shrub tundra consisting of a tall (up to 1 m) cover of woody shrubs (mainly *Betula* and *Salix* species) understoreyed by a dense cover of cotton grass tussocks, other sedges, forbs, dwarf shrub-heaths and mosses. This vegetation exhibits extremely high standing crop and aerial biomass values, approx. 2–3 times those of the Marion Island and other circumpolar tundra-type vegetations and greater even than those of many tropical savannahs.

Alpine shrub and meadow communities exhibit much lower above-ground biomass and standing crop values than occur in the island vegetation although a maximum biomass value of 348 g m $^{-2}$ at one site on Mt Wyoming is reported (Scott and Billings, 1964), corresponding to an approximate above-ground standing crop of 1 038 g m $^{-2}$ (calculated by Dennis and Johnson, 1970, from the data of Scott and Billings, l.c.). This latter figure is roughly 40% lower than the overall vegetation standing crop on Marion Island. More than half of all sites investigated on Mt Wyoming, however, supported less than 200 g m $^{-2}$ of live material above-ground, while estimates from Mt Washington alpine tundra range between 81 and 208 g m $^{-2}$ (Bliss, 1962).

In contrast to the high above-ground standing crop the island vegetation contains far lower amounts of below-ground plant matter than do typical sub-Arctic low-shrub tundra vegetations. Low-Arctic tundras of sedges, mosses, lichens and shrubs, which exhibit low above-ground standing crops, possess below-ground standing crops comparable to that of the island vegetation. This accords with similar observations on South Georgia (Greene, et al., 1973) and on

Signy Island (Edwards, 1973) and supports Bliss's statement (Bliss, 1970) that the Arctic environment is relatively more severe for the above- than the below-ground parts of plants and that although annual below-ground production is lower in the Arctic than in more temperate regions, the roots live longer and decompose more slowly. This longer root life, coupled with a slower decomposition rate, means that the below-ground vegetation standing crops in the cold soils of northern circumpolar regions are often higher than in the warmer (and wetter) soils of Marion Island. Even in an Arctic tundra vegetation at Barrow, Alaska, which exhibits very low above-ground standing crops (112–266 g m⁻²), the amount of plant material below-ground (1 520–2 185 g m⁻²) is comparable to that of the island vegetation. Dennis and Johnson (1970) suggest that the subsurface standing crop at Barrow is large because there is almost no intervening above-ground woody tissues to act as a sink for excess photosynthates and that the root systems of the plants therefore act as such a sink.

The below-ground standing crop of alpine vegetation is lower than that of Marion Island and other tundra vegetations (Table 5) although a maximum for alpine vegetation of 3 634 g $\rm m^{-2}$ is reported on Mt Washington (Bliss, 1966).

3. Nutrient status of the vegetation

(a) Chemical composition of Marion Island plant species

It has been indicated (Table 2 and previous sections) that five vascular plant species are responsible for the bulk of the plant cover and overall standing crop of the island vegetation. The contents of mineral elements in the leaves, leaf litter and roots (or rhizomes) of these species are presented in Table 6. Also included are the mineral element contents of fronds of the moss *Brachythecium rutabulum*.

In common with other herbaceous plant species the most prominent ash element in the living portions of Marion Island plants is potassium. The nitrogen content in the leaves and roots is commonly less than twice the potassium content, in contrast to tundra plant species of the northern hemisphere in which the concentration of nitrogen is normally considerably higher (from three to ten times) than that of any ash element (Rodin and Bazilevich, 1967).

The contents of calcium in the island plants are low compared with those of most northern hemisphere tundra plant species (Rodin and Bazilevich, *l.c.*), reflecting the low calcium status of the island soils. The calcium content of *Acaena magellanica* leaves is higher than those of the other island plants indicating a greater requirement for this element by this species and partly explaining its luxuriant growth in the relatively calcium-rich soils under drainage-line communities (Table 3). *Acaena* plants occurring in drainage lines possess greater concentrations of calcium than do those growing in the other island plant communities (Smith, 1976), suggesting a calcium deficiency in the island soils.

The island plants possess high magnesium contents, a response to both the low soil calcium status and to influx of magnesium from the surrounding ocean. Very

Table 6

Concentrations of mineral elements (% of dry weight) in Marion Island plant species.

Species	Organ	Calcium	Magnesium	Sodium	Potassium	Iron	Nitrogen	Phosphorus
Blechnum penna-marina	leaf 15 litter 15 rhizome 10	5 0,43±0,038 6 0,81±0,087 0,33±0,020	0.70 ± 0.023 0.89 ± 0.020 0.39 ± 0.041	0.27 ± 0.050 0.12 ± 0.025 0.17 ± 0.052	$1,50\pm0,087$ $0,21\pm0,025$ $0,93\pm0,157$	$0,004\pm0,001$ $0,018\pm0,005$ $0,023\pm0,010$	2,47±0,130 1,88±0,101 1,32±0,147	0.25 ± 0.015 0.19 ± 0.012 0.25 ± 0.065
Acaena magellanica	leaf 8 litter 8 root 8	8 0,70±0,070 8 0,91±0,133 8 0,19±0,029	0.52 ± 0.043 0.54 ± 0.028 0.24 ± 0.037	$0,42\pm0.063$ $0,16\pm0.034$ $0,08\pm0.045$	$1,39\pm0,201$ $0,35\pm0,057$ $0,57\pm0,043$	0.015 ± 0.008 0.030 ± 0.018 0.021 ± 0.018	$2,03\pm0,101$ $2,00\pm0,190$ $0,95\pm0,041$	0.23 ± 0.016 0.18 ± 0.013 0.12 ± 0.021
Poa cookii	leaf 12 litter 8 root 7	$\begin{array}{c} 0.12\pm0.013 \\ 0.15\pm0.049 \\ 0.14\pm0.044 \end{array}$	0.08 ± 0.010 0.11 ± 0.012 0.13 ± 0.026	$0,26\pm0,053$ $0,09\pm0,031$ $0,25\pm0,071$	$1,26\pm0,105$ $0,15\pm0,070$ $0,43\pm0,053$	0,009±0,005 1,69±0,123 0,024±0,010 1,15±0,144 0,075±0,005 1,22±0,121	$1,69\pm0,123$ $1,15\pm0,144$ $1,22\pm0,121$	0.16 ± 0.010 0.11 ± 0.018 0.11 ± 0.017
Azorella selago	leaf 12 litter 12 root 8	0,47±0,073 0,55±0,041 0,42±0,063	0.33 ± 0.048 0.30 ± 0.049 0.38 ± 0.036	0.88 ± 0.140 0.04 ± 0.019 0.18 ± 0.034	$1,47 \pm 0,211$ $0,08 \pm 0,013$ $0,87 \pm 0,103$	1,47±0,211 0,018±0,005 1,47±0,127 0,08±0,013 0,114±0,055 1,11±0,101 0,87±0,103 0,017±0,005 1,33±0,035	$1,47\pm0,127$ $1,11\pm0,101$ $1,35\pm0,035$	$0,14\pm0,011$ $0,10\pm0,014$ $0,14\pm0,013$
Agrostis magellanica	leaf litter 4 root 2	4 0,13±0,030 4 0,16±0,056 2 0,22±0,307	0.19 ± 0.023 0.14 ± 0.015 0.28 ± 0.180	0.45 ± 0.374 0.12 ± 0.062 0.27 ± 0.266		1,01±0,517 0,007±0,003 1,90±0,891 0,18±0,214 0,022±0,011 0,95±0,279 0,51±0,438 N.D. 0,86±0,457	1.90 ± 0.891 0.95 ± 0.279 0.86 ± 0.457	0.16 ± 0.071 0.08 ± 0.038 0.17 ± 0.321
Brachythecium rutabulum	living frond	0,39±0,103	0,36±0,037	0,13±0,035	0,83±0,041	$7 0.39 \pm 0.103 0.36 \pm 0.037 0.13 \pm 0.035 0.83 \pm 0.041 0.045 \pm 0.020 1.81 \pm 0.136 0.17 \pm 0.044$	1,81±0,136	$0,17\pm0,044$

Values expressed as means \pm 95% confidence limits N = number of samples N.D. = not determined

heavy influx of sodium also occurs from this source and the plants characteristically contain high concentrations of this element. As demonstrated in Table 6, the concentration of sodium is second only to that of potassium amongst the ash elements in leaves of Azorella selago, Poa cookii and Agrostis magellanica. This is also true for the leaves of at least four other island plant species, Montia fontana L., Uncinia dikei, Juncus scheuchzerioides and Agrostis sp. cf. A. antarctica (preliminary, unpublished data). Both A. selago and P. cookii often form an important component of the vegetation in areas heavily influenced by wind-whipped salt-spray and occasional inundation by waves. Their salt tolerance may be related to an ability to tolerate high internal levels of sodium before suffering injury.

Although the exchangeable sodium status of the mire peat is low (Table 3) this is due to the inherently low retention capacity of colloidal active surfaces for the sodium ion. Proportionately, salt-spray has virtually the same ionic composition as sea-water (Malloch, 1972; Grobbelaar, 1975) and however slight the deposition of this salt-spray on the mire surfaces, because of the slow drainage from these areas, the mire soil solution can be expected to contain relatively higher proportions of sodium than of any other cation. This is substantiated by unpublished data (Grobbelaar, 1975, D.Sc. manuscript) on the ionic concentration of the island's soil solutions. Intensive leaching of sodium from surrounding slope areas also enriches the mire soil water in this element. It is likely, therefore, that the high sodium contents of the leaves of plants occurring predominantly in mire areas (Agrostis magellanica, J. scheuchzerioides, U. dikei and M. fontana) reflect the disproportionately high sodium concentration in the soil solution and may represent an adaptation enabling these plants to exploit the otherwise nutrient-poor mire substrate.

The mineral element content of the leaf litter of most island plant species differs from that of the corresponding leaf tissue in that there is a relative increase in calcium, magnesium and iron whereas there is an absolute decrease in the more mobile elements such as sodium, potassium, nitrogen and phosphorus (Table 6). The higher calcium and magnesium contents in the litter are most likely caused by the withdrawal of photosynthates from dying leaves resulting in a decrease in the dry weights of these leaves rather than to intrinsic increases in the amounts of the two elements in the actual dead leaf material.

Because the mire substrate is poor in available nutrients, the amounts of elements reabsorbed before leaf-death or leaf-fall may be critical to the success of plant species growing under the waterlogged, nutrient-deficient mire conditions. In this context it is of interest to note that the data in Table 6 indicates a greater reabsorption of sodium, nitrogen and phosphorus from dying leaves of *Agrostis magellanica* than from those of the other, non-mire, plant species, supporting the proposal (Small, 1972a; 1972b) that bog species subsist on relatively smaller amounts of nutrients than do plants in other habitats and that this is related to the

ability of the bog species to reabsorb a greater proportion of the nutrients from their leaves preceding leaf-fall than do non-bog species.

On Marion Island approximately 50% of Acaena magellanica leaf material which had senesced and died early in March 1974 was lost through decomposition by the first week in May of that year. Greene, et al. (1973) states that the decay of Acaena leaves on South Georgia is so rapid that over 90% of the litter is lost in three months as compared with a 25% loss in one year for Festuca erecta litter. At senescence there is an especially rapid decrease in the dry weights of Acaena leaves as the leaf carbohydrates are incorporated into the extensive perennial roots and stems of the plants. This decrease in leaf dry weight masks simultaneous losses of leaf nitrogen so that the resultant litter indicates the same nitrogen content per unit dry weight as does the living tissue. This high nitrogen content in Acaena leaf litter may be partly responsible for the observed rapid rates of decay of this material in the field.

TABLE 7.

Amounts of ash elements plus nitrogen (g m⁻²) contained in the plant matter of the Marion Island plant communities.

Community			Ab	ove-gro	und		Below-	Total
•		1	Biomass		Dead	Total	ground	in
		Vasc.	Cryp.	Total	O.M.	Above	Total	S.C.
Fernbrake	Ash elements	16,47		16,47	24,90	41,37	74,67	116,04
	N	11,48		11,48	20,76	32,24	52,17	84,41
	Ash elements + N	27,95		27,95	45,66	73,61	126,84	200,45
Open scrub	Ash elements	13,06		13,06	21,22	34,28	42,89	77,17
	N	7,96		7,96	19,25	27,21	30,88	58,09
	Ash elements + N	21,02		21,02	40,47	61,49	73,77	135,26
Drainage Line	Ash elements	20,66	4,13	24,79	11,26	36,05	34,20	70,25
	N	13,30	3,83	17,13	9,70	26,83	26,25	53,08
	Ash elements + N	33,96	7,96	41,92	20,96	62,88	60,45	123,33
Slope Crest	Ash elements	17,97		17,97	34,97	52,94	28,74	81,68
	N	12,32		12,32	38,13	50,45	25,66	76,11
	Ash elements + N	30,29		30,29	73,10	103,39	54,41	157,80
Tussock grassland	Ash elements	21,98	4,66	26,64	21,00	47,64	52,22	99,86
	N	15,38	4,46	19,84	25,42	45,26	43,88	89,14
	Ash elements + N	37,36	9,12	46,48	46,42	92,90	96,10	189,00
Mire	Ash elements	2,29	5,94	8,23	2,07	10,30	29,35	39,65
	N	2,24		7,73	2,80	10,53	17,40	27,93
	Ash elements + N	4,53	11,43	15,96	4,87	20,83	46,75	67,58
Fjaeldmark	Ash elements	7,07		7,07	18,74	25,81	18,39	44,20
	N	3,76		3,76	16,21	19,97	12,23	32,20
	Ash elements + N	10,83		10,83	34,95	45,78	30,62	76,24

(b) Contents of mineral elements in the standing crop components of the various plant communities

The amounts of ash elements plus nitrogen contained in the vegetation of the various island plant communities are presented in Table 7. In general, these amounts are approximately proportional to the standing crops of the respective communities. A disproportionately large amount of mineral elements is found in the fernbrake community, however, due to the high proportion of living green tissue (leaves of *Blechnum penna-marina*) in the standing crop of this community.

In proportion to their high standing crops, tussock grassland and slope-crest communities contain relatively low amounts of mineral elements. This is due to the importance of *Poa cookii* and *Azorella selago* leaf litter in the above-ground standing crop component and not to inherently low concentrations of mineral elements in the plants of the two communities. Smith (1976) has shown that most plants occurring in the tussock grassland community are in fact richer in nitrogen, phosphorus, potassium and iron than are plants of the same species occurring in the other plant communities.

Mire vegetation also contains a low amount of mineral elements in proportion to the standing crop, despite the fact that this vegetation consists wholly of graminoid and bryophyte species and that no perennial or non-green living tissue occurs in the above-ground component of the standing crop. Seventy-six per cent of the plant material in mire communities occurs below ground compared with corresponding values of 31–71% for the other island plant communities. This greater importance of the below-ground component, as well as low concentrations of mineral elements in the litter of mire-plant species (see previous section) is responsible for the low amounts of mineral elements contained in the standing crop of mire communities.

TABLE 8.

Amounts of mineral elements (kg ha⁻¹) contained in the standing crop components of Marion Island vegetation.

Element		Α	bove-grou	ınd		Below-	Total
	Vasc.	Biomass Cryp.	Total	Dead O.M.	Total Above	ground Total	in S.C.
Calcium	12,06	5,13	17,19	59,13	76,32	65,55	141,87
Magnesium	12,60	4,26	16,86	43,75	60,61	74,92	135,53
Sodium	15,86	1,23	17,09	8,35	25,44	49,09	74,53
Potassium	38,40	9,90	48,30	13,83	62,13	149,38	211,51
Iron	0,26	0,39	0,65	5,34	5,99	4,16	10,15
Phosphorus	5,70	1,72	7,42	12,08	19,50	39,18	58,68
Total ash elements	84,88	22,63	107,51	142,48	249,99	382,28	632,27
Nitrogen	56,65	19,92	76,57	128,93	205,50	257,24	462,74
Total mineral elements	141,53	42,55	184,08	271,41	455,49	639,52	1 095,01

(c) Overall standing crop of mineral elements in the island vegetation

The amounts of mineral elements contained in the vegetation standing crop of an average hectare of the island's low altitude black lava areas are presented in Table 8.

Because of the prominence of herbaceous and moss species in the island vegetation and in accordance with the data presented in Table 6 there is a predominance of potassium amongst the ash elements of this vegetation, despite substantial accumulation of calcium and magnesium in the dead, above-ground plant matter.

A total content of 1 095 kg ha⁻¹ of mineral elements accumulates in the plant matter of the island's low altitude terrestrial vegetation, 42% of which is attributable to nitrogen. This value is low compared with many northern hemisphere shrub tundras where, because of high below-ground standing crops, similar amounts of mineral elements may accumulate in the biomass component of the vegetation alone (Rodin and Bazilevich, 1968).

Whereas in typical shrub tundra vegetation the bulk (80%) of mineral elements is contained in the below-ground sphere (Rodin and Bazilevich, 1967) only 58% of the mineral elements incorporated in the island vegetation are located below ground. This is due to the relatively low below-ground standing crop of this vegetation and to the accumulation of sodium, magnesium and potassium in the above-ground plant organs due to influx of these metals from the surrounding ocean.

Conclusion

Marion Island is situated at a much lower latitude than are any of the northern circumpolar areas represented in Table 5. In addition, the moderating influence of the ocean dominates the island's climate, keeping the temperature fairly constant throughout the year (Table 1) and preventing the occurrence of bitterly cold weather. The length of the growing season and the air and soil temperature regimes on the island are consequently more conducive towards plant growth than are those of northern circumpolar tundra regions possessing a continental climate without the dampened seasonal effect of a surrounding ocean. In contrast to most of these circumpolar areas where permafrost is common and unfrozen soil water available for only a restricted period during the year, the soils of Marion Island have a plentiful water supply. In addition, these soils are highly organic and are deep and fine-textured, edaphic conditions favouring the development of maximum above-ground standing crops in alpine vegetation (Scott and Billings, 1964) and in sub-Arctic tundra (Pearsall and Newbould, 1957; Gorham, 1974).

These more favourable conditions for plant growth are reflected in the accumulation of large quantities of alive and dead above-ground vascular plant material in the Marion Island vegetation and cause the above-ground standing crop of this vegetation to be higher than that of comparable low-growing sub-Arctic and low

Arctic tundra vegetations despite the much higher biomass of cryptogams in the latter. This confirms previous observations that the above-ground standing crops of low altitude sub-Antarctic vegetations are higher than those of most other comparable northern hemisphere tundra vegetation types (Jenkin and Ashton, 1970; Huntley, 1972a; Wielgolaski, 1972a, 1972b; Green, *et al.*, 1973; Walton, 1973).

Although the high above-ground biomass of vascular plants on Marion and other sub-Antarctic islands indicates that environmental stresses are less severe on sub-Antarctic plant communities than on northern circumpolar tundra and alpine plant communities, it is not at present certain why such high above-ground standing crops develop in the vegetation of sub-Antarctic regions as compared with those of temperate and tropical grasslands. In addition to the long preservation of above-ground plant remains, Jenkin and Ashton (1970) postulate that the luxuriance of Macquarie Island grasslands is related to a long growing season, a relatively depressed temperature optimum for the plant species and a prolonged leaf longevity. On Marion Island the virtual absence of herbivores must play an important role in the development of the high standing crop of the lowland plant communities (Huntley, 1972a).

The predominance of green material and the *halophytic* nature of the island vegetation causes the above-ground biomass component of this vegetation to contain a disproportionately large amount of ash elements compared to most other tundra vegetation types. As indicated in Rodin and Bazilevich (1967) halophytic communities may accumulate very high values of chemical elements in their biomass, especially if this biomass is fairly large. The importance of the surrounding ocean on the accumulation of mineral elements by the island vegetation is demonstrated by the fact that 136 kg of mineral elements (including silica, manganese and aluminium) are contained in an above-ground biomass of 4 900 kg ha⁻¹ of a U.S.S.R. low-Arctic shrub tundra whereas the smaller biomass (3 900 kg ha⁻¹) of the island vegetation incorporates 184 kg of mineral elements, excluding the content of silica, manganese and aluminium (Rodin and Bazilevich, *l.c.*).

ACKNOWLEDGEMENTS

The South African Department of Transport sponsors the biological research programme on Marion Island. Professor E. M. van Zinderen Bakker, director of this programme, and Professor R. du T. Burger, Department of Soil Science, University of the Orange Free State, provided unstinting support and advice during the course of the investigation. Sincere thanks are due to them and to Professor C. D. Pigott, University of Lancaster, U.K., and Dr G. H. Wiltshire, Institute for Environmental Sciences, U.O.F.S., for criticism of this paper in manuscript.

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THE EFFECT OF BURROWING SPECIES OF *PROCELLARIDAE* ON THE NUTRIENT STATUS OF INLAND TUSSOCK GRASSLANDS ON MARION ISLAND

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ABSTRACT

On inland slopes of Marion Island the dominant *Blechnum penna-marina* fern carpet is replaced by luxuriant *Poa cookii-*dominated tussock grassland communities in areas where bird species of the *Procellariidae* establish burrows. Soils under these tussock grasslands have considerably higher contents of inorganic nitrogen and, in proportion to their organic carbon contents, of total phosphorus than do soils under other island plant communities. Plants growing in tussock grassland communities possess higher contents of nitrogen, phosphorus, potassium, iron and, to a lesser extent, sodium than do plants of the same species occurring in non-tussock grassland areas. These higher soil and plant nutrient contents are ascribed to manuring by the birds.

UITTREKSEL

DIE INVLOED VAN *PROCELLARIIDAE* SOORTE OP DIE MINERALE STATUS VAN BINNELANDSE POLGRASLANDE OP MARIONEILAND

Op Marioneiland word die dominante *Blechnum penna-marina* varingbedekking van die binnelandse hange deur 'n welige polgrasgemeenskap van *Poa cookii* verdring in gebiede waar voëls van die *Procellariidae* nesmaak. Grond van die polgrasgemeenskappe bevat 'n hoër anorganiese stikstofinhoud en, in verhouding met die organiese koolstofinhoud, 'n hoër fosforinhoud as grond wat onder ander plantgemeenskappe voorkom. Plante van die polgrasgemeenskappe is ryker aan stikstof, fosfor, kalium en yster, en in 'n mindere mate natrium, as plante van dieselfde spesies wat in nie-polgrasgemeenskappe groei. Die hoër mineraalkonsentrasie in die plante en grond van die polgrasgemeenskappe word aan bemesting deur voëls toegeskryf.

Introduction

Communities of large tussock-forming grasses of which *Poa* species are usually the most important dominants are characteristic features of the vegetation of southern ocean islands (Wace, 1960). Because these communities are most often best developed on sea-facing slopes close to the shore they have been considered by some workers to be halophytic and dependent upon exposure to salt-spray (Skottsberg, 1912, 1942; Cour, 1959). In most southern islands, however, tussock grassland communities are generally associated with penguin rookeries, seal

wallowing-grounds, albatross nests and other biotic influences (Taylor, 1975; Wace, 1960, 1961; Greene, 1964; Smith and Walton, 1975).

In the Maritime Antarctic Smith (1972) notes that Deschampsia antarctica Desv. on Signy Island (60° 43'S., 45° 38'W.), although not forming tussocks proper, is particularly luxuriant immediately below nests of snow petrels (Pagodroma nivea Forster) and cape pigeons (Fulmarus capensis L.) and also at the margins of areas disturbed by elephant seals (Mirounga leonina L.). In the sub-Antarctic region Greene (1964) mentions that although pure stands of closed tussock grassland on South Georgia (54° 16'S., 36° 36'W.) are best developed on gently sloping ground away from penguin and elephant seal colonies, on the steep hillsides of Bird Island (54°S., 38° 3'W.), colonies of black-browed and greyheaded albatrosses (Diomedea melanophrys Temminck and D. chrysostoma Forster) lead to the local development of open tussock and the manuring influence of these birds results in an increased lushness of the tussock. In Macquarie Island (54° 30'S., 158° 57'E.) tussock grasslands *Poa foliosa* Hook, f. forms different associations with several other plant species and the association occurring at any given site depends upon exposure to sea-spray, maturity of the soil and trampling effects of animals (Taylor, 1955; Gillham, 1961). In his summary of the factors affecting the occurrence of the P. foliosa associations, however, Taylor does not include biotic influences.

As early as the end of the last century Moseley (1892) stated that on Marion Island (46° 54'S., 37° 45'E.) "The grass (*Poa cookii* Hook.f.) is abundant everywhere, mingled with *Acaena* (*A. magellanica* (Lam.) Vahl.) and *Azorella* (*A. selago* Hook.f.)", and that "The plants are, no doubt, rendered especially luxuriant by the dung of the numerous sea-birds." Moseley also added the erroneous observation that "The *Poa cookii* nowhere forms tussocks." Huntley (1971) considers that the manuring influence of birds and seals is of more importance than salt-spray in determining the distribution of *Poa cookii* tussock grassland on Marion Island as stands of this community are frequently found several km from the coast, where salt-spray deposition is slight but where numerous burrows of nesting colonies of small petrels and prions (family *Procellariidae*) occur.

During the period 1971–4 an intensive investigation into the nutrient relationships of the plants and soils of Marion Island was carried out. In the course of this investigation it became obvious that there are marked differences in the soil and plant nutrient status of the inland tussock grassland communities and that of the other island plant communities. These differences, which are ascribed to the manuring influences of the burrowing bird species inhabiting the tussock grassland communities, are presented in this paper. As far as can be ascertained no previous investigations into the chemical aspects of the relationship between tussock grassland and the manuring influences of animals have been undertaken on islands of the southern ocean.

SITE AND METHODS

Descriptions of the climate, geology, topography and vegetation of Marion Island are provided in Van Zinderen Bakker Sr., Winterbottom and Dyer (1971) and Smith (1976). The analytical methods used in the determination of the mineral contents of the plants and the soils are outlined in detail in Smith (l.c.).

DISCUSSION AND RESULTS

Similar to those of many polar and circumpolar regions, the soils of Marion Island are deficient in nitrogen and phosphorus (Smith, 1976 and Table 1) and any mechanisms whereby these two elements are added to the soil system are manifested by marked increases in plant vitality and standing crop of the vegetation (Van Zinderen Bakker Jr., 1971). Areas surrounding elephant seal wallows and wandering albatross (*Diomedea exulans* L.) and giant petrel (*Macronectes giganteus* Gmelin and *M. halli* Mathews) nests support a luxuriant, dark-green *Poa cookii*-dominated vegetation which contrasts strikingly with the drab, yellow-green surroundings. The increased vitality of the influenced plants is directly correlated with increases in their nutrient contents due to excretion by these animals (Croome, R. L., unpublished 1971–2 expedition report).

The dominant plant cover of the well-drained slope areas of lowland black lava flows of Marion Island is that of a thick carpet of *Blechnum penna-marina* (Poir) Kuhn. On some protected slopes this fern carpet is replaced by a dense vegetation comprising luxuriant dark-green swards of *P. cookii* codominant with *Acaena magellanica* (Smith, 1976). A dense understorey of the moss *Brachythecium rutabulum* (Hedw.) B.S.G. occurs under the *Acaena* canopy and *Azorella selago* and *B. penna-marina* are common throughout this community, which has been termed *inland tussock grassland* by Huntley (1971) and which is invariably undermined by numerous burrows of small petrel and prion species.

Soils under these inland tussock grasslands have considerably higher contents of inorganic nitrogen (predominantly in the ammonium form) than do soils under plant communities not influenced by the birds (Table 1). It is felt that this is caused by addition of inorganic nitrogen to the tussock grassland soils through the bird excreta. In relation to their relatively low organic carbon values the total phosphorus content of these soils is also high, possibly indicating enrichment in inorganic phosphorus by the bird guano.

The total percentage base saturation of the tussock grassland soils is low compared with that of soils under other plant communities. This is principally due to lower exchangeable calcium and magnesium contents, which are associated with slightly lower pH values, in the tussock grassland soils. Tentatively, it is proposed that nitrification of the added ammonium ions in these soils causes the decrease in soil pH due to the reaction $2NH_4^+ + 4O_2 \rightarrow 2NO_3^- + 4H^+ + 2H_2O$ and that the newly formed nitrate ions are neutralized predominantly by calcium and magnesium to form soluble nitrate salts which are subsequently leached from the

TABLE 1 Chemical status of the horizons containing living roots in the soils under tussock grassland and non-tussock grassland plant communities.	% saturation of C. E. C. % % % mg/100 g soil Mg Na K Total OrgC Total N Total P NH4-N NO3-N	grassland 22 4,2-4,7 674 \pm 139,8 19 \pm 3,1 28 \pm 5,7 4 \pm 0,6 4 \pm 1,3 55 \pm 9,2 34,3 \pm 6,75 2,00 \pm 0,280 0,65 \pm 0,115 tr2,9 0,0-tr.
ussland plant	% Total P	0.65 ± 0.11
on-tussock gr	% Total N	$2,00 \pm 0,280$
ussland and n	% OrgC	34.3 ± 6.75
tussock gra	Total	55 ± 9.2
TABLE 1 Is under	E.C.	$4 \pm 1,3$
in the soi	tion of C Na	4 ± 0.6
ving roots	% saturation of C. E. C. Mg Na K	28 ± 5.7
taining li	Ca %	$19 \pm 3,1$
horizons con	% Water	74 ± 139.8
us of the l	Hd	4,2-4,7 6
ıl statı	z	22
Chemica	Plant Communities N pH N Non-tussock	grassland

 $8\ 4.0-4.1\ 360\pm 19.4\ 14\pm 0.9\ 13\pm 2.5\ 5\pm 1.8\ 1\pm 0.4\ 34\pm 3.4\ 25.0\pm 3.96\ 1.66\pm 0.249\ 1.55\pm 0.381\ 0.9-8.4\ 0.0-1.0$ grassland Tussock

Values expressed as ranges or as means \pm 95% confidence limits. N = number of determinations. tr. = trace (<1 mg/100 g soil).

upper soil horizons. This causes a further pH decrease and also explains the low calcium and magnesium status of soils under tussock grassland. This indirect evidence that nitrifying organisms are present, and are capable of functioning in the low pH-low temperature soil régime prevalent on the island, offers an interesting field for a microbiological investigation into the island's soil and peat deposits.

The exchangeable potassium status of these soils is very low, approximately 1%, corresponding to 0,1–0,4 m-equiv. of exchangeable potassium per 100 g of soil. Graley, Nicholls and Piper (1960) consider that soils possessing exchangeable potassium levels below 0,5 m-equiv. per 100 g soil may be suspect as being deficient in this element.

There are very marked differences in the nutrient status of tussock grassland and non-tussock grassland plants (Table 2). Dead and alive leaves of plants occurring in tussock grasslands have significantly higher contents of nitrogen, potassium, iron and, to a lesser degree, sodium than do plants of the same species from other, undisturbed plant communities.

Addition of nitrogen and phosphorus in the bird guano to the soils under tussock grasslands is probably directly responsible for the increased concentrations of these two elements in the plant leaves and also for the luxuriance and the high standing crops of tussock grassland communities (Smith, 1976). Potassium is involved in virtually every physiological function taking place within the plant (Ulrich and Ohki, 1966) and the increased concentration of this element in the roots and leaves of tussock grassland plants is thought to be a response to the greater plant vitality and growth caused by nitrogen and phosphorus fertilization rather than directly to addition of potassium to the system in the guano. It is of interest that the potassium content of the tussock grassland soils is lower than those of the soils under the other plant communities indicating that very little of this element is, in fact, added to the tussock grassland soils in the guano and that the increase in plant growth "forced" by the nitrogen and phosphorus fertilization causes increased plant uptake of potassium from a soil which can well be suspected as being deficient in this element.

No significant increases in soil sodium content due to manuring by the birds is evident in Table 1. The substantially higher sodium concentrations in some organs of the tussock grassland plants might therefore be a response to the low potassium concentrations of the underlying soils, as it is well known that in some plants partial replacement of potassium in the tissue may be assumed by sodium, especially where deficiencies of the former element occur (Ulrich and Ohki, 1966).

The concentrations of iron in alive and dead leaves of tussock grassland plants are consistently about two to three times higher than are those of plants of other slope areas, whereas no similar effect is apparent in the roots of the tussock grassland plants (Table 2). Early workers demonstrated the correlation between

Species & Organ

Poa cookii

Leaf

Site N

Calcium

Magnesium

TABLE 2

Comparison of the nutrient status of plants growing in inland tussock grassland and non-tussock grassland communities.

Nutrient Content (%)

Potassium

(1) 8 0.11 0.020 0.09 0.010 0.26 0.053 1.16 0.072 0.005 0.001 1.58 0.063 0.15 0.009

Iron

Mean C.L.

Nitrogen

Mean C.L.

Phosphorus

Mean C.L.

Sodium

Mean C.L. Mean C.L. Mean C.L. Mean C.L.

Leai	(2)										*0,005					
Leaf litter	(1) (2)										0,017 *0,036					
Root											0,076 0,074					
Acaena ma	igella	anic	ca													
Leaf	(1) (2)										0,008 *0,026					
Leaf litter	(1) (2)										0,016 *0,054					
Root											0,023 0,017					
Azorella se	elago	,														
Leaf											0,014 *0,025					
Leaf litter	(1) (2)										0,070 *0,202					
Root											0,018 0,014					
Blechnum	nenn	a-n	narina													
Leaf	(1)	11	0,44								0,004 0,004					
Leaf litter	(1) (2)										0,014					0,012 0,055
Rhizome	(1) (2)		. ,			. ,			. , .		0,025 0,020	. ,	, .	. ,	,	0,066 0,150
Brachytheo	ium	rut	abalum	!												
Living fronds											0,030 *0,065					
(I) = mea	n ele		ent con	centrat	ion ±		confide	ence li	mits (C	C.L.) ii	n plants	of no	n-tusso	ock gra	ssland	com-

(2) = mean element concentration \pm 95% confidence limits (C.L.) in tussock grassland plants.

* indicates that the differences between (1) and (2) are significant at P = 0.5.

N.D. = not determined.

iron concentration and chlorophyll content in plant tissue (Bolle-Jones and Notton, 1954; Jacobson and Oertli, 1965) and it is now well established that the chloroplasts contain most of the iron in the leaf (Granick, 1958). The healthier, darker-green colour of the plants of tussock grasslands and other biotically influenced areas has been mentioned and it is felt that these increases in plant-colour intensity and plant vitality are directly associated with the higher iron concentrations in the leaves of the tussock grassland plants. This is supported by the absence of high iron concentrations in the roots of these plants. The low pH values (Table 1) and substantial iron pans and sesquioxide deposits which exist in the island soils make it unlikely that any of these soils are iron-deficient and that the guano is therefore supplying an essential requirement of the plants for this element.

The data in Table 2 indicates that Acaena magellanica leaves from tussock grasslands possess lower amounts of calcium than do those of non-tussock grassland communities. This is partly a reflection of the lower calcium status of the soils under tussock grassland (Table 1). A. magellanica, however, occurs abundantly in wet drainage-line communities which overlie (relatively) calciumrich soils (Smith, 1976) and plants from these communities have high calcium contents. These high contents are principally responsible for the observed differences between the leaf-calcium status of tussock grassland and non-tussock grassland Acaena plants.

ACKNOWLEDGEMENTS

This investigation was sponsored by the South African Department of Transport. Thanks are due to Professor R. du T. Burger, Department of Soil Science, University of the O.F.S. for advice and criticisms during the investigation and to Professor E. M. van Zinderen Bakker, director of the Marion Island biological research programme for criticisms of this paper in manuscript.

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STUDIES IN CYPERACEAE IN SOUTHERN AFRICA: 7. CYPERUS PROLIFER LAM. A CASE OF MISTAKEN IDENTITY

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ABSTRACT

A review of the history of the names *C. prolifer* Lam. and *C. isocladus* Kunth revealed that *C. isocladus* Kunth should be regarded as a synonym of *C. prolifer* Lam. and that much of the S.A. material hitherto identified as *C. isocladus* Kunth is more correctly assigned the name *C. prolifer* Lam.

UITTREKSEL

STUDIES VAN CYPERACEAE IN SUIDELIKE AFRIKA: CYPERUS PROLIFER LAM. 'N GEVAL VAN IDENTITEITSVERGISSING.

'n Historiese ondersoek van die name C. prolifer Lam. en C. isocladus Kunth dui aan dat C. isocladus Kunth 'n sinoniem van C. prolifer is, en dat meeste van die Suid-Afrikaanse versamelings voorheen bekend as C. isocladus Kunth, werklik C. prolifer is.

Clarke (1897), in a footnote to his description of *Cyperus isocladus* Kunth, commented that "C. prolifer Lam. (C. aequalis Vahl), is a frequent plant in SE. Tropical Africa and the Mascarene Islands, and has the stem trigonous or nearly terete at the top. From this C. isocladus only differs in its triquetrous stem." He remarked further that, while Boeckeler may be justified in regarding these two as synonyms, he preferred to retain them as separate taxa. Certainly, it is evident that the growing collection of sedges from Natal and Zululand includes two taxa which are conveniently identified as "C. prolifer" and "C. isocladus" on the basis of Clarke's description and key, but the measure of doubt evident in Clarke's comments and the somewhat anomalous situation of the epithet "prolifer" applied to material which did not exhibit proliferations, prompted a careful review of the literature to establish the criteria on which these two should be distinguished.

C. prolifer Lam. was described on the basis of a collection by Joseph Martin from Mauritius. The holotype is a single flowering culm, without underground portions, bearing a dense, spherical umbel with an estimated 161 inflorescence rays most of which terminate in depauperate spikelets. Proliferating spikelets and at least two leafy proliferations from the axils of involucral bracts are present.

The description is brief, but includes two salient features "culmo triquetro" and "spiculis proliferis". The description of culm shape was undoubtedly prompted

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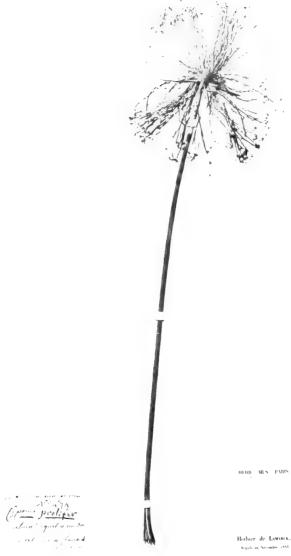


Fig. 1. The holotype of $Cyperus\ prolifer\ Lam.\ (ex\ Paris).$

by a note "culmo triquetro" which was certainly written by the collector, Joseph Martin (Raynal, 1970, personal communication), and in the French description is translated as a "tige trigone". It is not possible to assess the true shape of the culm in the original herbarium sheet and we must accept the collector's and author's opinions that the culm was three-angled.

Vahl (1806), citing Lamarck's reference and specimen, emphasized the relative lengths of the umbel branches by using the epithet "aequalis" thus drawing attention to the equal rays. Poiret (1806) also cited Lamarck's reference and specimen and again referred to "triangular" culms, but called the taxon C. papyroides.

There were, therefore, three epithets applied to a single taxon which was characterized by many equal rays, proliferations and leafless culms described as "triquetro" (that is three-angled with acute angles and concave faces), in the Latin description and "triangular to three-angled" in the French translations. It is perhaps in this minute difference that subsequent confusion and divergence of opinion arose, for in 1837, Kunth in descriptions of the culms, distinguished between C. aequalis (citing C. prolifer Lam. and C. papyroides Poir. as synonyms) and C. isocladus Kunth principally on features of culm shape. Kunth regarded the culm of C. aequalis as roughly terete or bluntly trigonous and that of C. isocladus as triquetrous – ironically the very term Lamarck used in the protologue of C. prolifer. This character has subsequently been used as the distinction between C. isocladus and C. prolifer or C. aequalis in all the later classifications.

A careful review of this early literature and a comparison of terms, illustrations, the type of *C. prolifer* Lam. and an isotype of *C. isocladus* Kunth prompts the following observations.

C. prolifer Lam., though it was given a very brief protologue, cannot be rejected in favour of a more preferable epithet. Thus Vahl's epithet "aequalis" and Poiret's "papyroides", though appropriate, descriptive and evocative, are, by the present code of nomenclature, invalid.

C. prolifer Lam. is clearly described as having triquetrous stems and, therefore, Kunth's decision to separate C. isocladus from C. prolifer on this very feature cannot be justified and C. isocladus must be relegated to a synonym. This opinion was most particularly reinforced when the isotype of C. isocladus was examined in Paris Herbarium and proved to exhibit the spherical multi-rayed umbel characters of C. prolifer Lam. as well as a triangular to triquetrous culm.

It is obvious that Kunth (1837) was aware of variation in culm shape in this taxon. In his opinion, the differences between the extremes of expression warranted specific recognition. In our opinion, even if such a distinction was warranted, the name *C. prolifer* Lam. should have been retained for that moiety with triquetrous stems.

In tracing subsequent taxonomic treatments it becomes apparent that when

variation of culm shape is accorded significance at specific level, Kunth's distinction between a triquetrous-culmed *C. isocladus* and a trigonous-culmed *C. prolifer* was gradually modified until the epithet ''prolifer'' became associated with terete-culmed specimens and ''isocladus'' applied to those with triquetrous culms.

Boeckeler (1862–4) accepted *C. aequalis* Vahl without referring to synonyms, but he placed *C. isocladus* Kunth as a variety of *C. aequalis*. In his study of *C. aequalis* Vahl, Boeckeler (1862–4) described the culm as "terete below, a little compressed to evidently trigonous or triquetrous at the apex". Boeckeler succinctly remarked that stem shape was unreliable. This pertinent observation was either overlooked or not followed up in later work and this variation in culm shape is very probably the reason for much of the nomenclatural confusion in this taxon.

Clarke (1883) recorded *C. aequalis* Vahl from Madagascar and retained this name in subsequent works (1884), but in 1885 included *C. prolifer* Lam. and *C. isocladus* Kunth in *Conspectus Florae Africae*. Discrepancies in the identification of cited specimens when compared with Kükenthal's citations reflect the difficulties and ambiguities in the character separating these two taxa.

Clarke (1883, 1884) referred to *C. aequalis* Vahl, but in 1895 more correctly used the older valid name *C. prolifer* Lam. In this Conspectus, however, he also included *C. isocladus* Kunth suggesting that he followed Kunth in distinguishing the two species.

Clarke (1897) expressed doubt about the validity of a distinction between *C. isocladus* and *C. prolifer*, but as has been shown above, regarded *C. prolifer* as the correct name for the specimens with round or terete culms. This, of course, entirely contradicts Lamarck's original description. Kükenthal (1936) although recognizing these two taxa as varieties and not species, still retained the association of the epithet "prolifer" with plants with terete culms. Kükenthal's illustration of *C. prolifer* Lam. is of particular interest for it bears a remarkable resemblance to the type specimen of *C. prolifer* and is unmistakably of the same phenotype as plants from South African collections erroneously identified as *C. isocladus* Kunth.

The undue emphasis on a single, and we believe, variable feature has caused a metamorphosis in the circumscription of the characters of *C. prolifer* Lam. which began by being described as having triquetrous culms, but which is now regarded as having terete culms.

After examining the type specimens of *C. prolifer* Lam. and *C. isocladus* Kunth (and living populations in Natal and Mauritius), and studying the descriptions in chronological order, tracing the gradual modifications and changes in emphasis, we have concluded that *C. isocladus* Kunth must be regarded as a synonym of *C. prolifer* Lam. If, after due consideration of all morphological features, a second taxon is to be recognized, it should be given a new epithet.

Cyperus prolifer Lam., Tab. Encyc. Meth. Bot. **1:** 147 (1791); Schum. in Engl., Pflanzenr. Ost-Afr. C: 119 (1895); Clarke in Dur. & Schinz, Consp. Fl. Afr. **5:** 572 (1895); in Dyer Fl. Cap. **7:** 176 (1897) and in Fl. Trop. Afr. **8:** 339 (1901); Kükenthal in Engl., Pflanzenr. **101:** 11, 256–7 (1936); Koyama in J. Taiwan Mus. **XIV** (3, 4): 174–5 (1961) Type: "Insula Franciae" (Mauritius), *Jos Martin 474* (P!)

C. papyroides Poir., Encycl. VIII: 270 (1806) ex herb. Lam.

C. aequalis Vahl Enum. Pl. 11: 320 (1806); Roem. and Schult. Syst. Veg. 11: 179 (1817); Spreng., Syst. Veg. 1: 220 (1825); Kunth, Enum. Pl. 2: 37 (1837); Krauss in Flora 28: 754 (1845); Steud., Synops. Pl. 2 (7): 22 (1855); Boeck. in Peters Reise Mossamb. Bot. 11: 538 (1862–4); in Linnaea XXXV: 557–8 (1868) and in Abh. Naturw. Ver. 7: 37 (1880–2); Bak. in Fl. Maurit: 412 (1877); Clarke in Journ. Linn. Soc. Lond. XX: 287 (1883) and XXI: 123 (1884); Chermez. in Ann. Mus. colon. Marseille XXX. 3. Sér vol. X: 12 (1922) and in Humbert Fl. Madag. 11: 69 (1937) ex herb. Lam. Papyrus aequalis Bojer in Hort. Maurit: 381 (1837) ex herb. Lam.

C. isocladus Kunth., Enum. Pl. 2: (1837); Drège & E. Mey., Zwei Pflanzen. Doc. 177 (1843) (as "jocladus"); Drège & E. Mey., *l.c.* 155, 157 (1843) (as "iocladus"); Steud., Synops. Pl. 2 (7): 22 (1855); Clarke in Dur. & Schinz. Consp. Fl. Afr. 5: 565 (1895); in Dyer Fl. Cap. 7: 175 (1897) and in Fl. Trop. Afr. 8: 339 (1901) Type: "Omsamwubo et Omsamcaba" (Cape Province), Drège 4431b (isotype P!)

C. esculentus Drège & E. Mey., Zwei Pflanzen. Doc. 177 (1843) non L. sensu stricto. (Drège 4431b.)

Perennial, erect or nodding, 23-105 cm high, in large clumps: rhizome horizontal, rarely vertical, ligneous; internode 0,6-3,1 × 0,2-0,6 cm, clothed by many-nerved, red-brown, persistent sheaths: leaves limited to sheaths; sheaths $4,5-26,5 \times 0,4-2,4$ cm, glabrous, many-nerved, nerves converging at apex, margin of mouth scarious; blades generally absent: culms triquetrous to terete, mainly triangular, glabrous: inflorescence bud ovoid, up to 4,6 cm long: involucral bracts 3, subtending rays, not exceeding inflorescence; inflorescence 5,6-18 × 5-15,5 cm; rays 101-259, umbellate, up to 16 cm long, forming reflex angle with culm apex, sheathed at base by tubular prophylls, 0,9 cm long: capillary rays occasional; ray receptacle globose: spikelets 1-30 per ray, 6-17 × 1-1,5 mm, generally flat, elliptic to narrowly ovate, yellow-brown to red-brown, darkening on drying and age: rhachilla straight, yellow-brown: glumes lowermost 1-3 sterile, remainder fertile, $1,2-1,7 \times 0,2-0,4$ mm, broadly ovate, base truncate, glabrous, yellow-brown, margin scarious, keel three-nerved, central nerve excurrent into mucron, 0,1 mm long: stamens 3; anthers $1,2 \times 0,2$ mm, yellow-brown, crested; filament as long as anther, pallid, with small red-brown markings: style 0,3 mm long, pale yellow-brown; style branches three, 1,2 mm long, dark brown, papillate: achene 0,4 × 0,2 mm, obovate, trigonous in transverse section; outermost



 $FIG.\ 2.$ A recent gathering of $\ensuremath{\textit{Cyperus prolifer}}\ Lam.\ from\ the\ South\ Coast\ of\ Natal.$

cells rectangular, with markedly sinuous margins. Flowering period November to May inclusive.

KENYA—Kwale district: Shimba hills, Mkadara, -.7.1939, Someren 18 (K); Matuga, -.11.1961, Bogdan 5352 (K); Lama district, Marrarani, Boni Forest, 1961, Gillespie 364 (K); Tanga district, Mombasa Waterworks. -.1.1934, Gibson 5 (K).

TANZANIA—Bagamoyo district, Mapinga, -.12.1915, Peter 14812 (K); Ndago, Bana Forest Reserve, -.8.1968, Shabani 166 (K); Kilwa district, Kilwa, -.6.1932, Schlieben 2353 (K); Lushoto district, Masinde, -.8.1937, Greenway 5142 (K); Manga district, -.7.1960, Haerdi 5830 (K); Mikindani district, -.3.1963, Richards 17790 (K). Rufiji district, Mafia Island, -.3.1933, Wallace 830 (K); Usaramo district, Dar-es-Salaam, -.6.1966, Wheeler Haines 4188 (K); near Dar-es-Salaam, -.11.1915, Peter 14854 (K); Kurasini, -.2.1971, Batty 1234 (K). ZANZIBAR ISLAND—.-.1847, Boivin s.n. (K); -.4.1867, Kirk s.n. (K); -.9.1868, Kirk s.n. (K); -.9.1873, Hildebrandt 1006 (K); -.4.1892 Sacleux 1823 (K); -.9.1894, Kuntze 206 (K); -.1.1929 Greenway 1175 (K); -.-.1931, Vaughan 1259 (K); 1863 (K); -.8.1950, Williams 59 (K).

PEMBA ISLAND-Kinazini, -. 3.1952, Williams 135 (K).

MOÇAMBIQUE—Beira district, Beira, -.12.1906, Swynnerton 931 (K); Road to Moebede, -.1.1948, Faulkner 181 (K); Gaza district, Chonguene, Campo de Ensaios, -.7.1949, Myre (K, NU); Inhambane district, entre Inhambane e Miramar, -.9.1948, Myre and de Carvalho 185 (K, NU); Lourenço Marques district, N. Inhaca Island, Delagoa Bay, -.7.1959, Watnough 389 (K); Quelimane district, -.8.1950, Munch 260 (K).

MADAGASCAR—-.-.1841, Perville 660 (K); -.-.1867, Boivin s.n. (K); Beravi -.7.1879 Hildebrandt 3069 (K); Central -.10.1881, Baron 479 (K); -.10.1882, Baron 1437, 1545 (K); North-west, -.-.1887, Baron 5240, 5504 (K); Betriraha, -.12.1889, Scott-Elliot 2218 (K); -.-.1889, Baron 5440 (K); -.5.1912, Methuen s.n. (K); Majunga, Marovoay, -.6.1912, Afzelius s.n. (K); Tmerimandrose, -.6.1921, Decary 418 (K); -.11.1930, Lam & Meeuse 5540 (K); Fort Dauphin, -.10.1932, Decary 10796 (K); Anivorano, -.11.1959 Schlieben 8044 (K).

MAURITIUS—-.-.1837, Bojer/Bouton s.n. (MAU); -.10.1862, Ayres s.n. (K); -.-.1864, Bouton s.n. (K); -.-.1867, Fl. Mauritius 1 (K); -.-.1892, Bojer s.n. (K); -.-.1892, Fl. Mauritius 8 (K); Vaughan 7B (K); -.2.1931, Vaughan s.n. (MAU); Midlands, -.1.1953, Rochecouste s.n. (MAU); Pandr d'Or, -.1.1954, Rochecouste s.n. (MAU); Wiehe s.n. (MAU); border of Perrier Nature Reserve, -.3.1973, Baijnath 856 (IU, MAU); in Perrier Nature Reserve, -.3.1973, Baijnath 857 (IU, MAU); Midlands, -.3.1973, Baijnath 865 (IU, MAU).

NATAL—2632 (Bella Vista): near Maputa and Big Kosi Lake (-CD), -5.1948, Rodin 4672 (K).

- —2732 (Ubombo): Ingwavuma, Kosi Bay (-AA), -.9.1961, *Edwards 2560* (K); Lake Sibayi (-BC), -.2.1958, *Tinley 68* (NH, NPB); Mpangazi Lake (-CA), -.1.1964, *Strey and Huntley 5023* (NU, PRE).
- —2831 (Nkandala): Eshowe (-CD), -.4.1949, Lawn 544 (NH); Mtunzini, Ngoya Mountain (-DD), -.-.1962, Venter 109 (NU); Ngoye, -.3.1907, Wood 10421 (NH, PRE); Ongoye area, -.9.1956, F. Bayer s.n. (NU); Garland's Farm, -.11.1969, Baijnath 659 (IU); Umlalazi Nature Reserve (-DD), -.5.1919, Mogg 4310 (PRE); -.1.1959, Guy and Ward 55, (K, NH, NPB); -.1.1964, Huntley 817 (PRE); Isingisi Lake, -.5.1955, Ward 2608 (NH, NPB. NU).
- —2832 (Mtubatuba): Dukuduku (-AA), -.9.1964, *Strey 5567* (NU, PRE); Ubisana Valley, -.7.1962, *Venter 80* (NU); Mpati (-AD), -.11.1969, *Baijnath 663* (IU); Richards Bay (-CC), -.1.1949, *Ward 715* (NU, PRE).
- —2930 (Pietermaritzburg): Inanda (-DB), -.7.1881, Wood 1331 (K); Durban (-DD), -.2.1883, Rehmann 8623 (K); Clairmont, -.2.1887, Wood s.n. (K, NH); Clairwood Race Course, -.2.1969, Baijnath 667 (IU); Merebank East, -.8.1965, Ward 5266 (NU, PRE); Merebank South West, -.8.1969, Baijnath 625 (IU); ponds near Umlaas River, -.-.1840, Krauss 165 (K); Isipingo North, -.8.1948, Ward 469 (NU).
- ---2931 (Stanger): Talmadges Pan (-BA), -.11.1969, *Baijnath 657* (IU); Greenwood Park (-CC), -.1.1914, *Wood 1016* (PRE).
- —3030 (Port Shepstone): Scottburgh South (-BC), -.2.1970, Baijnath 703 (IU); Umzinto, Umzinto-Park Rynie Road, -.2.1970, Baijnath 682 (IU); Ellingham Farm, -.2.1970, Baijnath 698 (IU); Park Rynie, roadside, -.2.1970, Baijnath 701 (IU); Park Rynie Beach, -.2.1970, Baijnath 702 (IU); Marburg, off Harding Road (-CB), -.1.1970, Ganga 1 (IU); -.2.1970, Strey 9562 (K); Shelley Beach (-CD), -.5.1970, Baijnath 745, 748 (IU); Margate, -.2.1931, Rump s.n. (NH); -.2.1967, Nicholson 479 (NH); Southbroom (4 km south of Ramsgate), -.2.1970, Baijnath 718 (IU); Palm Beach area, -.2.1970, Baijnath 720 (IU); Hibberdene, Umhlungwa River south (-DA), -.11.1971, Baijnath 838 (IU); Turton, Umfazazaan River south (S. of Isipofu turn-off), -.2.1970, Baijnath, 710, 715 (IU); Anerley, -.2.1970, Baijnath 716 (IU).
- -3130 (Port Edward Garage (-AA), -.2.1970, Baijnath 721 (IU).
- C. prolifer occurs on the eastern and south-eastern coasts of Africa and on several islands off the east coast of Africa and appears to be a tropical species which extends to a southern limit in the vicinity of the Umzimvubu River. Its distribution may well be limited by the influence of the warm Aghulhas Current. Populations in Natal are all from low-lying areas, the highest being 100 m above sea-level (Adams Mission).

The species is hygrophilous, preferring well-aerated habitats near streams or drinking holes with running water where, in the absence of competition, it may form dense stands resembling beds of diminutive papyrus. *C. prolifer* is, however, intolerant of shading and of stagnant conditions and if drainage is severely

impeded, the population exhibits sterile inflorescences and considerable vegetative reproduction in the form of proliferations from bract axils or ray tips. If stagnation is prolonged, the population may be restricted to the fringes of the stagnant area. If culms are trampled or lodged by floods, the plants multiply by vegetative proliferation within a short while.

In Natal, there appear to be two similar, possibly related taxa, which are described in the following paper (Baijnath, 1976).

ACKNOWLEDGEMENTS

Grateful appreciation is extended to the Directors of Herbaria for the loan of material for this study; to Mr Raynal for his interest and assistance and to the Director of the Herbarium, Paris for the loan of the type specimen of C. prolifer Lam.: to Mrs Mulder for technical assistance and to Dr K. D. Gordon-Gray for her helpful comments on the preparation of the manuscript.

One of us (H.B.) acknowledges with gratitude the financial support of the South African Council for Scientific and Industrial Research and the South African Sugar Association, and a Travel Grant to Mauritius from the S.C.D.I.F.A. and Maistry Educational Trusts.

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BOOK REVIEWS

WILD FLOWERS OF NATAL (COASTAL REGION), by Janet M. Gibson, with pp. $(180\times240 \text{ mm})$ xi, 1-136+116 full page colour plates, and numerous pencil sketches, Natal Publishing Trust Fund, 1975, R15.00.

After many years without a popular book on their native flowers, the wild flower enthusiasts in Natal are now faced with a choice of two books; one by Janet M. Gibson and the other by Barbara Jeppe. Like Jeppe's book, this book of Gibson's is essentially one for

popular consumption and for the student botanist.

In this most recent book, some 810 species from the Natal coastal belt have been illustrated. In addition, some species (76) have been illustrated twice to show both flowers and fruits, or the range of variation that occurs. These species represent a good crosssection of both families and individuals from the region covered. The text is very simple, consisting of only a few lines on each species; with comments on habit, habitat, flowering time and other points of interest. This brief text has allowed for a most pleasing layout, as the text for each colour plate is on the facing page. The arrangement of species follows that of the recently published Flora of Natal by Ross, so much so that the page numbers where each description occurs in Ross is given in the text as well as the generic number. This means that Gibson's and Ross's books can be used together, which is a considerable advantage.

The book is very well indexed with separate indices to common names, scientific

names and the national list of tree numbers.

The quality of binding, printing and reproduction of the book is excellent, making this

book a printing masterpiece.

All the colour illustrations have been reduced 50% from life size, which has added to the clarity and crispness of each sketch. The author has her own charming style of painting, albeit a little stiff, and writing, which makes this book rather unique when compared with similar, more recent books on South African plants.

E. Moll.

Grasses of Southern Africa, by Lucy K. A. Chippindall, with pp. 970, and 240 full page line drawings. Salisbury: M. O. Collins (Pvt.) Ltd. Rh \$48,00; R68,00; U.S.A. \$88,00.

The publishers describe this as "Something NEW in Scientific Publication". The format certainly is new for Southern Africa, as is the option of paying for the 24 units in ten monthly instalments. (Rh \$4,90; R7,00; U.S.A. \$9,00).

Each grass is dealt with in a four-page unit, punched to fit into a well-made binder, supplied with each set of 80 units - a total of three binders in all. Their overall size is convenient for field-work and the punch-holes look as though they will stand up to hard usage. Libraries will be able to staple the units together before binding them in book form.

The print and paper are excellent and, apart from the list of grasses issued with the first set, typographical errors are minimal. A complete index of latin and common names is to be

Supplied with the last set, the latter surely a prodigious undertaking.

Those who have worked with Lucy Chippindall's "A Guide to the Identification of Parameter South Africa in 1955. Grasses in South Africa" published in The Grasses and Pastures of South Africa in 1955, will not be disappointed in these far more detailed descriptions. It is obvious that Lucy Chippindall and her husband. A. O. Crook, have done an enormous amount of research and travelled widely to provide such comprehensive data. Each species is described in such a way as to make identification relatively easy. For each species there is a full page line-drawing, a map showing geographical distribution and interesting notes on economic value. Notes on how to recognise the species are particularly clear. Several artists are responsible for the clear and attractive drawings and there is a pleasing similarity of style. There are also useful drawings to illustrate the glossary. The schematic sketch of an "exploded" grass spikelet will be very helpful to those who do not know the intricacies of a grass spikelet. In the neighbouring sketch two arrows have been misplaced but this printing error should be obvious to all.

A special feature of the publication is the comprehensive list of common names for each species. For example, *Cynodon dactylon* has at least sixty! The compilation of these names must have entailed a great deal of research and the authors are to be congratulated on

including names used overseas as well as in several African countries.

The right-hand edges of pages 1 and 3 of each unit are panelled to show, in diagramatic form, the type of flowerhead, habit, habitat, soil and altitude range of each species and whether it is an annual or perennial species. A detailed key to the panels is provided. The authors hope that users of the book will be able to supply any missing data.

This can then be incorporated in future editions.

There are approximately 1 000 grass species in Southern Africa which mean that rather less than a third have been described in detail. However, species with the widest distribution or greatest ecological importance have been included. The low percentage is therefore not as limiting to field workers as to taxonomists. The loose-leaf form of publication means new units can be added from time to time and this we trust the authors will do.

The one obvious ommission is the provision of a key, however artificial, to the species described. Presumably workers will group the units according to flower head, habitat or genus and not according to the numbers allocated. But even so I visualise a great

"thumbing through" of the three volumes to find a required species!

This work is a timely contribution when our attention is once again drawn to the seriousness of our "vanishing grasslands" vide J. P. H. Acocks and the editorial in the June '76 issue of African Wildlife. It is vital in a country which is "80% veld that cannot be used for anything but grazing" for botanists, ecologists and those who manage this veld to work together to become familiar with individual grass species. This they will be able to do, very adequately, for at least the 240 species described in this book.

Paul INF Fairal I.

EMBRYOLOGY OF JUBAEOPSIS CAFFRA BECC.: 3. ENDOSPERM AND EMBRYOGENY

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ABSTRACT

Initially the endosperm is free nuclear, but in the mature seed it is cellular. Wall formation, which results from cell plate formation, is initiated when the embryo is between 32 and 64 cells large.

The zygote of *J. caffra* undergoes a post-fertilization rest period of between 30 and 70 days prior to division. Embryogeny, which is of the Asterad Type (*Muscari* Variation) is discussed in terms of the systems of Johansen and Souéges. A recapitulatory table for the first four cell generations is presented.

UITTREKSEL

EMBRIOLOGIE VAN *JUBAEOPSIS CAFFRA* BECC.: 3. ENDOSPERM EN EMBRIOGENIE

Aanvanklik is die endosperm vry-nukleêr maar in die volwasse saad is dit sellulêr. Wandvorming, wat as gevolg van selplaat ontwikkeling geskied, is geïnisieer wanneer die embrio uit tussen 32 en 64 selle bestaan.

Na bevrugting ondergaan die sigoot van *J. caffra* 'n rusperiode van tussen 30 en 70 dae voordat dit verder deel. Embriogenie, wat van die Asterad Tipe (*Muscari* Variasie) is, word in terme van die sisteme van beide Johansen en Souéges bespreek. 'n Rekapitulasietabel vir die eerste vier selgenerasies word voorgestel.

Introduction

Currently available literature pertaining to *Jubaeopsis caffra* deals almost exclusively with the distribution and general morphology of this species (Beccari, 1913; Marloth, 1915; Long, 1950; Barry, 1957; Story, 1959; Wager, 1968; Wicht, 1969; Palmer & Pitman, 1972; Robertson & Visagie, 1975). The only available data concerning embryological aspects of *J. caffra* are in respect of sporogenesis and gametogenesis (Robertson, a, b, 1976), and to date, nothing on its embryogeny has been published.

In all the reported cases concerning the endosperm of palms generally, it is initially nuclear (Davis, 1966) but subsequently becomes cellular. Some variations do exist in respect of the extent to which the endosperm becomes cellular and the transition from nuclear to cellular endosperm is not complete in all species. In *Cocos nucifera* for example, a large percentage of the endosperm remains in a liquid state, i.e. free nuclear (Cutter, Wilson & Freeman, 1955). In *Areca catechu* on the other hand, the entire mass of nuclear endosperm develops into a very hard cellular tissue (Datta, 1955).

Two conflicting reports concerning the endosperm found in *J. caffra* have been published. Marloth (1915) states that the mature seed is without milk, i.e. without nuclear endosperm. Story (1959) disagrees and claims that, just like the coconut, nuclear endosperm is found in the mature *J. caffra* seed.

When discussing the endosperm of palms, the question of ruminations or of ruminate endosperm naturally arises. Again, certain species exhibit this characteristic, e.g. *Areca catechu* (Venkato Rao, 1955) while many others do not.

The development of the palm embryo is still a virtually uninvestigated field of study. By 1950 (Johansen, 1950) the Palmae were embryogenically totally unknown. Subsequent to Johansen's classic publication, a small number of descriptions concerning the embryogeny of the Palmae have become available.

According to Venkato Rao (1958) the embryo development of both *Actinophloeus macarthii* and *Areca catechu* is of the *Trifolium* variation of the Onagrad Type (Johansen, 1950). In this type the basal cell, cb, of the two celled pro-embryo forms the suspensor only and does not contribute to the components of the embryo proper.

Guignard (1961) on the other hand, studied the embryogeny of *Chamaerops humilis* L. and describes the embryo development as belonging to the First Period Megarchtype IV with a Series Al tetrad in the second cell generation (Souéges 1939, 1948, & 1951, cited by Crété, 1963). This is in fact the first description of an embryo in which the basal cell of the 2-celled proembryo divides by means of a longitudinal wall during the formation of the cells of the second generation. Davis (1966) describes the embryogeny of *Chamaerops* as being of the Asterad Type (Johansen, 1950). Strictly speaking this is incorrect as the proembryo tetrad (second cell generation) of the Asterad Type comprises three tiers: two juxtaposed cells which originate from ca in the 2-celled proembryo; and two superposed cells (m and ci) which originate from cb of the 2-celled proembryo. Johansen's (1950) system for classifying embryonomic types does in fact not provide for a case where the basal cell of the first cell generation divides by means of a vertical or longitudinal wall.

The question concerning embryonomic types in general and the classification thereof is still very much an open question and is dealt with further in the discussion.

In this study three aspects of the embryogeny of *J. caffra* were investigated, viz. embryogenesis, embryotectonics and embryogenergy. For the classification of the embryonomic type both Johansen's and Souéges' systems were used. Furthermore, a comparative study of the size and rate of growth of the fruit and the development of the embryo was made.

MATERIAL AND METHODS

Female flowers and fruits were collected at various developmental stages from a cultivated tree in St. George's Park, Port Elizabeth. This material was fixed and

stored in Craf II (Sass, 1958) prior to dehydration in an ethyl alcohol/tertiary butyl alcohol (TBA) series. Thereafter it was infiltrated with and embedded in paraffin wax (55°C).

Lignification of the endocarp made it impossible to study embryogeny without prior removal of the embryo from the seed. This was achieved by firstly removing the fibrous exo – and mesocarp and then excising the embryo through the single functional germination pore. (Only one ovule remains functional and thus only one germination pore penetrates through the stony endocarp).

The embedded material was sectioned at 10 μ m on a rotary microtome as prescribed by Brooks, Bradley and Anderson (1950) and stained in safranin/fast green (Holtzhausen, 1972).

RESULTS AND DISCUSSION

Endosperm

The fertilization of the secondary nucleus by one of the male gametes results in the formation of the primary endosperm nucleus. (Fusion of the two polar nuclei occurs prior to fertilization.) This nucleus divides without the formation of a cell wall and consequently the endosperm of J. caffra is of the nuclear type. Development of the endosperm is initiated some considerable time prior to division of the zygote.

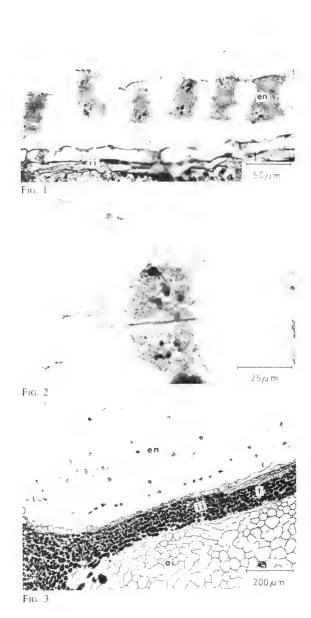
The endosperm nuclei become organised in a thin peripheral layer while the central zone of the embryo sac is filled with a mass of colourless cell sap (Fig. 1). In the mature fruit the peripherally placed endosperm is comprised of a cellular tissue while the central liquid mass becomes absorbed and makes way for a large cavity.

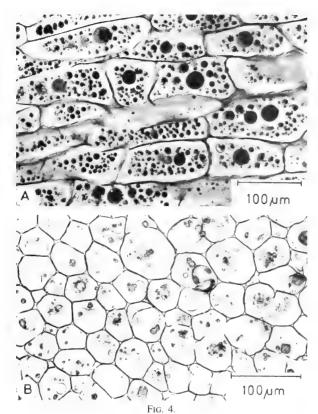
Division of the nuclei of the endosperm *Cocos nucifera* has been interpreted in various ways. Dutt (1954) and Datta, *née* Dutt (1955) report regular mitotic divisions in the endosperm nuclei, while Cutter and Freeman (1955, cited by Maheshwari, 1963) state that division of these nuclei occurs by means of nuclear fragmentation or amitotic division.

In *J. caffra* there is no doubt that division takes place by means of regular mitotic division (Fig. 2). Figure 1 shows that the division of the nuclei in the peripheral layer appears to be more or less synchronous.

Cell-wall formation in the endosperm is not initiated until the embryo has reached the 32 to 64-celled stage. This is in contrast to some of the other palms, e.g. *Actinophloeus* where the endosperm already becomes cellular at about the eight to ten-celled proembryo stage (Venkato Rao, 1958). Also different is the mode of wall formation. In *Actinophloeus*, the endosperm initially becomes cellular by a process of vacuolation and thereafter by cell plate formation (Venkato Rao, 1958) while in *J. caffra* the very first cell walls result from cell plate formation (Fig. 2).

The divisions are mainly periclinal in relation to the embryo sac wall (Fig. 2)





Endosperm of a mature *J. caffra* seed. A—Transverse section through the kernel. B—Tangential section through the kernel.

and result in a rather uniform layer of cells being formed. In a young fruit the peripheral endosperm cells are relatively small while the cells towards the middle of the endosperm are somewhat larger and radially elongated (Fig. 3).

Fig. 1.

Free-nuclear endosperm in a young J. caffra fruit (en—endosperm; ii—inner integument).

Fig. 2.

Periclinal division in an endosperm nucleus showing the formation of the cell plate.

Fig. 3

Cellular endosperm in the immature fruit of *J. caffra* (en—endosperm; ii—inner integument; oi—outer integument; t—tanniniferous layer).

The endosperm cell walls in an immature fruit are thin. As the fruit matures, the cellulose walls become only slightly thicker (Fig. 4) but never become as thick as the walls of the endosperm in *Phoenix dactylifera* (Lloyd, 1910). In a transverse section through the endosperm kernel, the cells are radially elongated, but in tangential section they are more or less isodiametric (Figs 4A & B). The cells of the mature endosperm are filled with droplets of oil and rhomboidal crystals.

The findings of this study regarding the absorption of the central mass of cell sap prior to maturation of the fruit, are contrary to those of Story (1959) who states that the mature fruit contains liquid endosperm or "milk", but confirms the view of Marloth (1915) who reports that the mature *J. caffra* fruit is without "milk".

Embryogeny

The data obtained in this respect are discussed below in terms of the embryonomic "classification systems" of both Johansen (1950) and Souéges (Crété, 1963).

It is felt necessary though that the systems themselves be briefly considered prior to applying them to the results of this study.

Both systems are based on the same embryonomic laws and principles and both make use of the tetrad structure and the role of the basal cell, cb, of the 2-celled proembryo in the construction of the embryo and its components as criteria for distinguishing between the various embryonomic types. One can but agree with Johansen (1950) when he regrets that these two systems (which were developed concurrently and independently of each other) were not incorporated into one.

It is not possible, and would certainly at this stage, be unwise to say which of these two systems is the better.

That of Johansen (1950) is excellent in that basically it is a relatively simple system and includes only six types of embryonomic development. These differ from each other with respect to the structure of the proembryo tetrad in the second cell generation and in the role played by the basal cell of the 2-celled proembryo in the construction of the embryo proper and its basic constituents. Each of these six types are in turn divided into an unspecified, and theoretically, unlimited number of variations.

The latter aspect is perhaps the weakness in Johansen's system. He admits that

Fertilization of the egg cell by the male gamete (fn—female nucleus; mn—male nucleus).

FIG. 5.

FIG. 6.

A-F—Longitudinal sections through proembryo at various stages of development (cf. Fig. 7). G—Longitudinal section through an embryo showing differentiation of the plumule and radicle tip. H—Transverse section through an embryo at a similar stage of development as the embryo depicted in Fig. 6G. I—Longitudinal section through a mature embryo.

⁽c—cotyledon; pl—plumule; pc—procambium; r—radicle; rc—rootcap; sy—synergid; z—zygote).

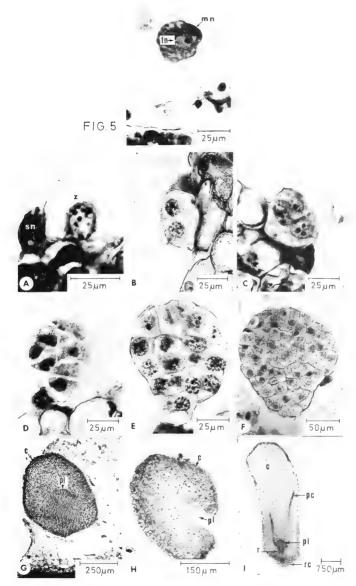


Fig. 6

not all variations are clearly definable and that some should in fact be dropped and that the species classified therein be added to some other variations. This system, it would seem, is thus not completely stable and will probably undergo various changes as more embryological data on more species become available.

Souéges' system is a very complex one and involves an unlimited number of periods, each of which is subdivided into six different groups or megarchtypes depending on the role played by the basal cell of the 2-celled proembryo in the formation of the embryo proper. Each of the megarchtypes is in turn subdivided into eight series and subseries on the basis of the proembryo tetrad formation and structure.

The disadvantage of this system is that it is too complex and clumsy. Its major advantage however, is that it is a stable system which provides for the incorporation of any future data without the basic layout or design of the system having to be changed.

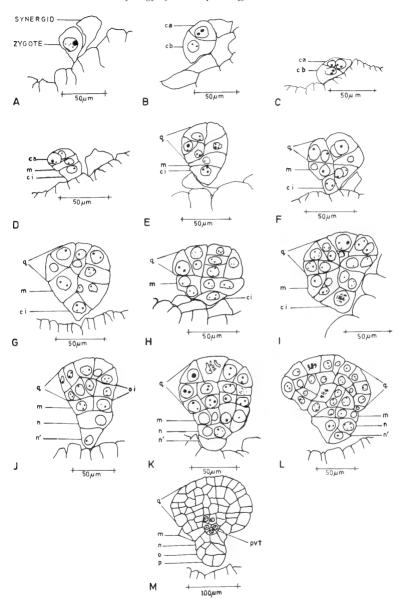
Fertilization (Fig. 5) of the egg cell of *J. caffra* by one of the male gametes results in the formation of a zygote (Figs 6A & 7A) which undergoes a rest period of between 30 and 70 days (Fig. 9). During this time, division of the primary endosperm nucleus occurs. The zygote is surrounded by a thin cellulose membrane and is spherical in shape. Degeneration of the one remaining synergid becomes evident from this stage onwards.

First Cell Generation

As is the case in virtually all investigated Angiosperms (Maheshwari, 1950) the first division of the zygote is transverse (Figs 6B, 7B), resulting in a proembryo comprised of two superposed cells, viz. a terminal cell and a basal cell. Being of the first period, these cells are designated ca and cb respectively. (The terminal cell refers to that one which is orientated furthest away from the micropyle while the basal cell is the cell closest to the micropyle.) This stage (Fig. 8A) represents the first cell generation.

Second Cell Generation

This generation, which is governed by the law of dispositions, is the most important with regard to the establishment of the embryonic type of *J. caffra*, because it is the generation in which the proembryo tetrad is formed. The terminal cell, ca, divides longitudinally and consequently a three-celled proembryo is formed. This proembryo consists of two juxtaposed cells in the upper tier and the single basal cell, cb in the lower tier (Figs 6C, 7C). Shortly thereafter, cb divides transversely to produce two superposed daughter cells m and ci. At this stage the proembryo is comprised of four cells arranged in three tiers, viz. ca, comprising two cells and tiers m and ci, each consisting of a single cell (Figs 7D, 8B). This



stage constitutes the proembryo tetrad of the second cell generation. The structure of this tetrad makes it possible at this stage to classify the embryonic type as being either of the Onagrad or the Asterad Types (Johansen, 1950). In terms of Souéges' periodic megarch system, the tetrad would belong to the first period of the A2 (filamentous) series.

Third Cell Generation

Although this generation is usually characterized by eight cells, the law of numbers often intervenes to bring about variations (Maheshwari, 1963).

The two cells in the upper tier (ca) of the tetrad divide by means of longitudinal walls to produce a single tier q, of four cells.

The middle cell m, also undergoes a longitudinal division to form a two-celled tier while tier ci remains undivided (Figs 7E, 7F).

In some cases the divisions resulting in the formation of q precede those in tier m, while in other cases, m divided before the cells in the upper tier (cf. Figs 7E, 7F).

Thus the third cell generation of *J. caffra* consists of seven cells arranged in three tiers, viz. q (four cells), m (two cells) and ci (one cell) (Fig. 8C).

Fourth Cell Generation

The quadrant cells of tier q in the third cell generation each divide by a transverse wall (Figs 7G, 7H) to produce an octant consisting of two tiers (oi and os) of four cells each. Concurrently the two cells constituting tier m in the third cell generation (Fig. 8C) both divide longitudinally (Fig. 7G) to produce a 4-celled tier (Fig. 7H). Division of the single cell ci is somewhat retarded, but it does eventually divide transversely (Fig. 7I) to produce two superposed tiers, viz. n and n' (Fig. 7J).

The proembryo constituting the fourth cell generation thus originates by the bipartitioning of each of the seven cells in the third cell generation and consequently it is comprised of 14 cells arranged in five tiers (Fig. 8D).

From the fourth cell generation onwards, the number of cells makes it extremely difficult to follow the precise pattern of cell divisions. It is possible though to follow the general development of each of the tiers, i.e. q, m, n and nw.

The cells of tier oi (Fig. 7J) divide transversely so that q consists of three tiers (Figs 6E, 7K). Thereafter, cell division in both oi and os occurs in both peri- and anticlinal directions and it becomes impossible to demarcate each tier of cells in q. At this stage a series of anticlinal divisions results in the formation of the dermatogen (Fig. 7L).

Cell divisions in tiers m, n and n' do not occur at the same rate as in q and no further divisions occur in these three tiers until the upper half of the proembryo is well developed (Fig. 7L). Subsequently n' divides transversely to produce two cells. The upper of these daughter cells constitutes tier o while the lower forms tier p. (Fig. 7M). Following this, the cells in p, o and n divide longitudinally while

those in m divide both longitudinally and transversely. It is at this stage that the first signs of differentiation of the stem's growth point, pvt, become evident in tier m (Figs 6B & 7M).

It is possible to predict the destinations of the various tiers which constitute the proembryo at this point. The growth point, the initials of the central cylinder of the root and the hypocotyl all originate from tier m while p forms the suspensor. Tier o will produce the root cap and the cells in tier n give rise to the initials of the root cortex while tier q produces the cotyledon.

The best way to summarize the embryonomy of *J. caffra* is by means of a recapitulatory table for the first four cell generations (using the abbreviations as prepared by Johansen (1950)).

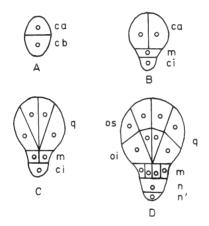


Fig. 8.

Schematic representations of the first four cell generations during the embryogeny of J. caffra flattened into a single plane. A—First cell generation; B—Second cell generation; C—Third cell generation; D—Fourth cell generation.

1. First Cell Generation (Fig. 8A)

Proembryo of two cells disposed in two tiers:

$$ca = pco$$

 $cb = phy + pvt + icc + iec + co + s$

Second Cell Generation (Fig. 8B)

$$ca = pco$$

 $m = phy + pvt + icc$
 $ci = iec + co + s$

Third Cell Generation (Fig. 8C)

Proembryo of seven cells disposed in three tiers:

$$q = pco$$

 $m = phy + pvt + icc$
 $ci = iec + co + s$

Fourth Cell Generation (Fig. 8D)

Proembryo of 14 cells disposed in four tiers:

$$q = pco$$

 $m = phy + pvt + icc$
 $n = iec$
 $n' = co + s$

It is clear from the above data that the basal cell cb, of the two-celled proembryo plays a substantial role in construction of the embryo components and consequently the embryonomy of *J. caffra* is of the Asterad Type and not the Onagrad Type (Johansen, 1950). The closest applicable variation of this type is the *Muscari* Variation (Johansen, 1950).

However, in the typical *Muscari* Variation, division of ci into n and n' occurs during the third cell generation. So, too, the division of n' into o and p take place during the course of the fourth cell generation. The third cell generation of *Muscari* therefore consists of eight cells in four tiers and the fourth cell generation of 16 cells in five tiers. Consequently the recapitulatory table for these two generations of *Muscari* are as follows:

```
m = phy + pvt + icc

n = iec

n' = co + s

4. q = pco

m = phy + pvt + icc

n = iec

o = co

p = s
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3. q = pco

(Johansen, 1950)

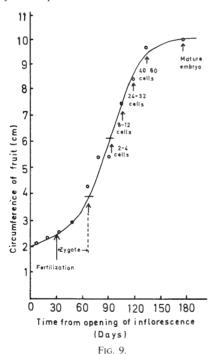
As already mentioned above, the formation of tiers n and n' from ci is retarded in *J. caffra* and delayed until the fourth cell generation while the division of n' occurs somewhat later than the fourth cell generation. The result is that the recapitulatory tables of these two genera, i.e. *Muscari* and *Jubaeopsis* appear quite different.

The fact that the embryogeny of J. caffra and Muscari is basically the same, but

that they differ with respect to cell numbers in the third and fourth cell generations as shown in their recapitulatory tables, raises two questions.

Firstly, to what extent should the embryogeny of two species differ before they can be classified into two different variations? Secondly, can the creation of a new variation of Asterad Type for *J. caffra* be justified?

The first question reflects the weakness of Johansen's system because no fixed criteria exist. The creation of a new variation would depend entirely on the personal opinion of the individual researcher and consequently no standard application of the system is possible.



Fruit growth in relation to the development of the embryo of *J. caffra*.

It is in this respect that Souéges' system of an infinite number of periods and six basic megarchtypes is perhaps to be preferred. The megarchtypes are defined on the basis of the destination of the basal cell of the two-celled proembryo. Both Jubaeopsis and Muscari are of the first period, both belong to Megarchtype 1 where cb = pvt + phy + icc + iec + co + s and both have a series A2 tetrad, (i.e. T-shaped) in the second cell generation. Consequently their embryogeny is

essentially the same and it is felt that in the event of their embryonomy being classified according to Johansen's system, they both be placed in the same variation, viz. the *Muscari* Variation of the Asterad Type.

Initially the development of the proembryo is extremely slow. As mentioned earlier, and as reflected in Fig. 9, the zygote undergoes a rest period of between 30 and 70 days. During this time though, fruit and endosperm development continues unabated.

By the time that the proembryo tetrad is formed, i.e. 90 days after the opening of the inflorescence, the fruit has already reached 60 per cent of its mature size (Fig. 9). During the next 45 days, development in the proembryo is somewhat faster, but still remains slow in relation to fruit development and by the time that the fruit has reached approximately 95 per cent of its final size, the proembryo exists as an undifferentiated, more or less globular, 64-celled structure (Fig.9).

From this point on however, i.e. during the last 45 days of development, growth of the fruit virtually ceases, while growth and differentiation of the embryo increase tremendously. During this period, the growth points of both the stem and radicle become fully differentiated and the cotyledon develops.

Maturation of both the fruit and embryo is preceded by the absorption of the central mass of cell sap or "milk" which is initially present in the endospermal cavity.

CONCLUSIONS

While the majority of palms have nuclear endosperm, there seems to be some difference in the manner by which the endosperm becomes cellular. In *J. caffra* the free-nuclear condition is apparently terminated by wall formation, resulting from cell-plates. No ruminations occur.

The results of this study indicate that Story's (1959) report concerning the presence of endosperm "milk" in the mature fruit, is incorrect.

As far as the embryogeny is concerned it appears from the data accumulated in this study that it is of the Asterad Type and specifically of the *Muscari* Variation if classified according to Johansen (1950) or of the first period, Megarchtype 1 with a Series A2 tetrad in the second cell generation in terms of the system of Souéges (Crété, 1963). Unfortunately very little information with respect to the embryogeny of other palms is available and no comparisons are possible. It appears though that the embryogeny of the Palmae is very divergent and in view of the fact that such a small number of palm species have been studied in this respect, it would seem that a study of the embryogeny of genera from the various subfamilies would be both enlightening and well justified.

ACKNOWLEDGEMENTS

The writer is indebted to the University of Port Elizabeth and the C.S.I.R. for their financial support of this project.

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DIE SUID-AFRIKAANSE SPESIES VAN HOMOGLOSSUM

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UITTREKSEL

Vir hierdie hersiening van die Suid-Afrikaanse spesies van *Homoglossum* Salisb. (Iridaceae) is herbariummateriaal en lewende plante uit hul natuurlike habitats ondersoek. Die anatomiese ondersoek van veral die blaarstruktuur en struktuur van die knoltunicae het bruikbare differensiële kenmerke opgelewer. Sitologiese ondersoek het min bygedra. Die genus word in drie seksies ingedeel en tien spesies word erken. Geïllustreerde beskrywings, die geografiese verspreiding en die sinonimie van die spesies word gegee, asook 'n sleutel vir hul uitkenning.

Alle moontlike kenmerkverskille tussen *Homoglossum* en die naverwante *Gladiolus* is nagegaan. Daar is besluit om *Homoglossum* as aparte genus te handhaaf, hoewel dit van *Gladiolus* slegs in die vorm van sy perigonium verskil. *H. aureum* word teruggeplaas na *Gladiolus*

ABSTRACT

THE SOUTH AFRICAN SPECIES OF HOMOGLOSSUM

Herbarium material and living plants from their natural habitats were studied for this revision of the South African species of *Homoglossum* Salisb. (Iridaceae). Anatomical investigations of the leaves and corm tunics provided useful diagnostic characters, but cytological investigations were disappointing. The genus is divided into three sections and ten species are recognized. Illustrated descriptions of the species, their geographical distribution and synonymy are given, and a key is provided.

The difference between *Homoglossum* and the closely related *Gladiolus* was reinvestigated. Although the only difference found is in the shape of the perianth, it has been decided to keep *Homoglossum* distinct from *Gladiolus*. *H. aureum* is transferred back to *Gladiolus*.

INLEIDING

Homoglossum Salisb. is 'n klein genus van die Iridaceae en is inheems in Afrika. Dit kom veral voor in die suidwestelike winterreënstreek en die suidelike distrikte van die Kaapprovinsie van Suid-Afrika. Enkele spesies is ook vir Sentraal-Afrika aangemeld.

In die laat negentiende eeu is *Homoglossum*-spesies meestal onder *Antholyza* geplaas, maar Brown (1932) toon die onjuistheid van hierdie siening aan en plaas die genus weer selfstandig, soos Salisbury gedoen het. Die genus is naverwant aan *Gladiolus* en Baker (1892) het dit as deel van hierdie genus beskou, terwyl Goldblatt (1971) dit slegs 'n "genus of convenience" noem. In hul monografie oor *Gladiolus* sonder Lewis, Obermeyer en Barnard (1972) *Homoglossum* van *Gladiolus* af.

Vir publikasie aanvaar 20 Augustus, 1976.

Om uitsluitsel te verkry of *Homoglossum* apart van *Gladiolus* beskou behoort te word, en omdat die laaste verwerking van die genus meer as 40 jaar gelede gedoen is (Brown, 1932) en daar skynbaar meer spesiesbeskrywings as ware spesies is, is die uitgebreide hersiening van die genus onderneem.

Herbariummateriaal uit die vernaamste binnelandse en buitelandse herbaria wat tipe-eksemplare besit (sien onder BEDANKINGS) is bestudeer. Vars materiaal van al die Suid-Afrikaanse spesies, met die uitsondering van één, is versamel vir anatomiese en sitologiese studies, om die morfologiese onderskeidingskenmerke aan te vul. Daar vars materiaal van die Sentraal-Afrikaanse spesies nie verkry kon word nie, is hierdie soorte nie ondersoek nie.

Morfologie

Habitus—Die plante is geofiete met 'n klein ondergrondse gerokte knol en 'n slanke regop spruit van 30 cm tot meer as 1 m hoog.

Aan die begin van die groeiseisoen (herfs) verskyn 'n groep bywortels vanuit die knolbasis, en kort daarna die spruit uit 'n okselknop naby die knoltop. Die spruit bestaan uit 'n lang, dun, meestal regop stingel met drie, of soms meer, lang smal loofblare wat die stingel tot naby die terminale aar omsluit met buisvormige blaarskedes. Vegetatief stem *Homoglossum* ooreen met die groep *Unifoliati* van die genus *Gladiolus* (Lewis e.a., 1972).

Die blomperiode is vanaf April (H. priorii, H. merianellum) tot November (H. fourcadei). Vanaf September tot Desember, afhangende van die spesie, is die doosvrugte ryp en word die sade versprei, en droog die spruit uit. Die plante oorleef die lang, droë somer deur middel van die nuwe knol wat gedurende die groeiseisoen ontwikkel om die ou knol wat sy voedsel afgegee het vir die vorming van die spruit te vervang.

Die gerokte knol—Dit is simmetries, afgerond aan die basis en effens puntig bo. Dit bestaan uit twee internodia en het, soos die tipiese knolle van die meeste Ixieae, 'n smal sentrale stele met 'n breë setmeel-bevattende skors rondom en 'n bedekking van een of meer tunicae. Die kring bywortels wat aan die begin van die groeiseisoen uit die knolbasis spruit, bly funksionerend tot die einde van die groeiseisoen, selfs nadat die knol sy voedsel afgegee het en verkrimp is.

Die bogrondse spruit ontwikkel uit die hoogste okselknop van die knol. Die basis daarvan swel geleidelik op en vorm die nuwe knol. Die groei van die plant is dus simpodiaal, met die nuwe knol vereers effens skeef bo-op die oue geplaas, maar later skynbaar mediaan daarop.

Die hooftunica wat die hele knol bedek, is die geslote, blywende basis van die onderste katafil, wat verbreed namate die jong knol opswel. Die tweede katafil groei uit die nodus naby die middel van die knol en vorm 'n keëlvormige tunica oor die boonste gedeelte daarvan. Die eerste loofblaar groei vanaf die nodus aan die top van die knol.

Die tunicae is van waarde om die spesies in groepe in te deel. Daar is twee

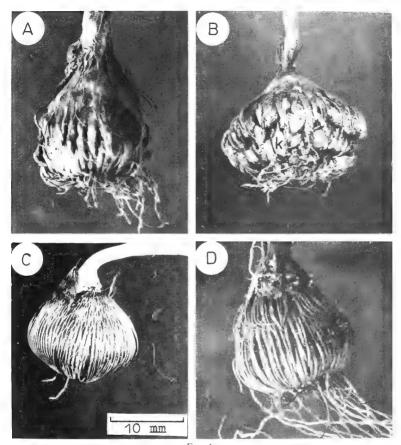


FIG. 1.

Gerokte knolle van *Homoglossum*-spesies: A. B., *H. watsonium*; C, *H. priorii*; D, *H. merianellum* var. *aureum*; k, byknolle.

tipes, met 'n oorgangsvorm tussenin: (a) By *H. watsonium* (Fig. 1A) en *H. muirii* is die tunica dik, hard en verhout en splits dit vanaf die knolbasis na die middel in harde, platterige, skerppuntige slippe 1–2 mm breed; in die boonste gedeelte is dit ongesplits en glad. (b) By die meeste spesies, te wete *H. abbreviatum*, *H. fourcadei*, *H. guthriei*, *H. priorii*, *H. quadrangulare* en *H. vandermerwei* is die tunicae membraneus en taamlik sag en splits dit van onder na die middel van die knol, in fyn, filiforme, min of meer parallelle fibrille wat ongeveer 0,5 mm in dwarssnee is; bo die middel is die tunica ongesplits met 'n opgehewe veselstring-

netwerk daarop (Fig. 1C). (c) Twee spesies, te wete *H. huttonii* en *H. merianellum* (Fig. 1D), het tunicae met elsvormige, taamlik harde fibrille wat intermediêr in dikte is tussen die bogenoemde tipes en by *H. huttonii* in deursnee varieer van 0,5 tot 0,8 mm. Ongelukkig is baie herbariumeksemplare sonder knolle en daarom is hierdie kenmerk wat die knoltunicae bied, van beperkte waarde.

Talle klein, sittende byknolle (Fig. 1B) ontwikkel by *H. watsonium* in die katafil-oksel aan die basis van die knol. Hulle skei maklik van die knol en sommige ontwikkel tot selfstandige plante. Hulle stem ooreen met die byknolle van bv. *Gladiolus natalensis* (Lewis *e.a.*, 1972). Ondergrondse stolons met byknolle aan hul punte is nie gevind nie.

Een of 'n paar krimpwortels mag uit die basis van die nuwe ontwikkelende knol groei, veral by jong plante wat te vlak in die grond staan.

Die stingel—Dit is onvertak, behalwe by H. vandermerwei waar dit aan die basis van die aar mag vertak.

Tot naby die aar is die stingel styf omsluit deur die buisvormige blaarskedes van die basale en die tweede loofblaar, asook, naby die basis, van die skedevormige katafille.

Die blare—Die plante is heterofil; die loofblare verskil in vorm en grootte en is distieg of soms effens spirodistieg gerangskik.

Aan die basis van die stingel is twee of soms drie laagteblare (katafils) van 5 tot 25 cm in lengte, wat uit buisvormige blaarskedes bestaan: die eerste is die kortste en is membraanagtig; die tweede en derde is fyn gerib en groen na bo, wat aantoon dat hul toppe bo die grond verskyn. Hulle is naak, behalwe vir die boonste katafil van *H. merianellum*.

Die basale loofblaar, geheg aan 'n nodus naby die top van die knol, is meestal baie lank, soms langer as die bloeistingel. By *H. priorii*, *H. merianellum* en *H. guthriei* is dit egter korter. Sy blaarskede is groen, fyn gerib, buisvormig, en is soms tot 25 cm lank en dikwels langer as die lamina.

Die lamina van hierdie blaar is smal en unifasiaal, en verskil in vorm by die spesiesgroepe: by *H. priorii*, *H. merianellum* en *H. guthriei* is dit lineêr, meestal met twee tot vier (of na die basis meer en na die top minder) effens opgehewe, met sklerenchiem versterkte are en met sklerenchiemrande (Fig. 2A-C). By *H. watsonium* is die rande besonder sterk en verbreed, en is daar in die middel van die lamina een sterk opgehewe sklerenchiemstrook (''middelaar'') wat egter smaller is as die sklerenchimatiese rande (Fig. 2E). Hierdeur kan die spesie geredelik uitgeken word, al is sy kenmerkende knol afwesig. Die lamina van *H. vandermerwei* ressorteer ook onder hierdie tipe, met dié verskille dat die blare meer is en dikwels effens breër en sagter as by *H. watsonium*, met smaller sklerenchiemstroke (Fig. 2D).

By *H. quadrangulare*, *H. huttonii*, *H. fourcadei* en *H. abbreviatum* het die smal lamina vier ewe breë, in die lengte verlopende vleuels, met hul rande verbreed deur sklerenchiemribbe (Fig. 2F) wat in 'n dwarssnee na 'n Griekse kruis lyk. Na

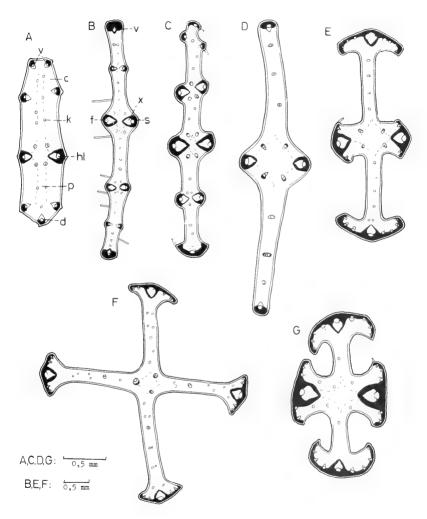


Fig. 2.

Dwarssneë deur die unifasiale loofblare van die *Homoglossum*-spesies, gesny op ongeveer die middelhoogte: A, *H. priorii*; B, *H. merianellum* var. *aureum*; C, *H. guthriei*; D, *H. vandermerwei*; E, *H. watsonium*; F, *H. quadrangulare*; G, *H. mairii*; c, chlorenchiem; d, dorsale mediane vaatbundel; floëem; hl, hooflaterale vaatbundel; k, klein vaatbundels met enkele xileem- en floëemelemente; p, kleurlose parenchiem; s, sklerenchiem; v, ventrale vaatbundel(s); x, xileem.

die top van die blaar word die vleuels smaller sodat die blaar vierhoekig vertoon, en in die droë toestand nagenoeg tereet, maar met vier diep lengtegroewe. By *H. muirii* is die hele lamina smal en pseudotereet (Fig. 2G) met vier lengtegroewe, net soos by die toppe van die bogenoemdes.

Die tweede loofblaar, 'n stingelblaar, besit meestal 'n langer blaarskede as die eerste; maar die lamina is heelwat korter en slegs aan die punt unifasiaal en soortgelyk aan die lamina van die eerste. As die eerste loofblaar van 'n herbariumeksemplaar verlore is, kan die vorm daarvan tog nog met taamlike sekerheid vasgestel word deur die tweede blaar se punt as maatstaf te gebruik. So is gevind dat die blare van die tipes van *H. acuminatum* en *H. flexicaule* soortgelyk aan dié van *H. watsonium* moet wees.

Die derde loofblaar, en die andere as daar meer is, ontwikkel hoog op die stingel naby die aar en is gereduseer, korter en skutblaaragtig, met 'n kort skede en 'n lamina wat vir sy grootste gedeelte bifasiaal is.

Slegs by een spesie, *H. merianellum*, is die blare behaard (Fig. 2B) met wit syagtige trichome afkomstig uit interkostale epidermisselle. Verskeie van die ander spesies het besonder klein, slegs met 'n lens sigbare, haarstompies op die rande van die kostale sklerenchiemstroke (Fig. 2C, E, G).

Die bloeiwyse—Die aar is los en besit meestal twee tot ses blomme, of soms tot tien (of selde slegs één) wat eensydig staan of in twee rye met 'n hoek van tot ongeveer 60° tussen die blomrye. Slegs by *H. vandermerwei* vertak die aar aan sy basis met een of twee takke wat effens later as die hooftak blom.

Die rachis is regop of, by sommige spesies, bv. *H. priorii*, *H. merianellum* en *H. fourcadei*, effens golwend. By *H. priorii*, *H. quadrangulare* en *H. watsonium* is dit soms horisontaal gebuig. Dit gebeur wanneer die ontwikkelende rachispunt tydelik vasgevang bly in die omklemmende blaarskede en die rachis dan tydens sy verlenging, boogvormig uitgroei. *H. acuminatum* wat slegs in sy horisontale rachis van *H. watsonium* verskil, kan dus nie as 'n aparte spesie gehandhaaf word nie.

Soos tipies vir die Ixieae, is elke blom aan sy basis omsluit in 'n twee-kleppige bloeiskede. Dit bestaan uit die stingelomvattende of half stingelomvattende skutblaar (bractea) aan die anterieure kant van die blom, en die skutblaartjie (bracteola) aan die posterieure kant, met sy rug teen die bloeistingel geadorseer. Beide is groen of rooigroen en het vry rande behalwe wanneer, by boë uitsondering, die rande van die bractea aan sy basis vir 'n paar millimeter vergroei is. Die bractea is groot en het meestal 'n baie smal, skaars sigbare, membraanagtige randjie, terwyl die bracteola, wat korter is as die bractea, 'n breër membraneuse rand het en klein-tweetandig aan sy top is; aanduidings van twee kiele is hier selde te sien. Dikwels is die bracteola gedeeltelik verberg deur die bractea, deur dieselfde torsie wat die blomme na die een kant van die aar draai.

Bo die eindblom het die rachis 'n smal, 15 mm lange verlenging met 'n klein bractea en bracteola en 'n onvolmaakte blom tussen hulle.

Die lengte van die bractea in verhouding tot die perigoniumbuis varieer: by die

meeste spesies is die bractea heelwat langer as die smal onderste gedeelte van die perigoniumbuis; by *H. merianellum* korter; en by *H. guthriei* is die twee dele min of meer ewe lank.

Die perigonium (blomdek)—Die vorm van die perigonium is die enigste diagnostiese kenmerk wat Homoglossum van Gladiolus onderskei. By die laasgenoemde is die perigoniumbuis tregtervormig en verbreed dit geleidelik na bo. By Homoglossum is die lang, krom perigoniumbuis in twee wydtes gedifferensieer (Fig. 3A): die basale gedeelte wat minder as die helfte van die buis se lengte beslaan, is smal buisvormig en ongeveer 1,5 tot 3 mm in deursnee; naby die middel van die buis verbreed dit skielik tot 'n effens sydelinks afgeplatte, silindriese gedeelte ongeveer 5 tot 8 mm in deursnee, wat byna konstant in breedte bly tot waar die perigoniumsegmente begin.

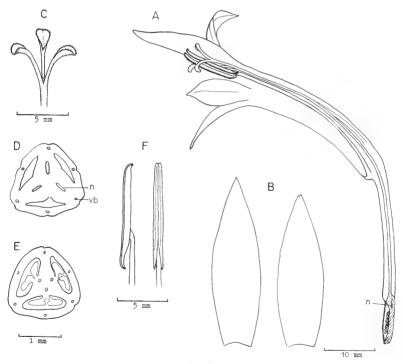


Fig. 3.

Die blom van *Homoglossum quadrangulare:* A, in die lengte gesny; B, bractea (links) en bracteola (regs); C, stempels; D, dwarssnee deur die top van die vrugbeginsel; E, dwarssnee deur die middel van die vrugbeginsel; F, helmknoppe van die kant en van voor gesien; n, nektarie; vb, vaatbundel.

Waar die buis verbreed, is by die meeste spesies, met die uitsondering van *H. huttonii*, *H. priorii* en *H. vandermerwei*, 'n ronde, vlak uitstulping na die anterieure kant van die blom, wat as 'n nektarversamelsakkie funksioneer. Die populêre naam, suikerkane, vir verskeie *Homoglossum*-spesies, is hieraan te wyte.

Die smal, basale buisgedeelte is reguit en staan meestal byna vertikaal. Hoërop is die buis na die anterieure kant gebuig, dikwels tot so 'n mate dat die segmente horisontaal staan of soms effens afhang. Uitsonderings is *H. huttonii* en *H. abbreviatum* waar die kromming van die buis min is en die blomme min of meer stygend.

Die blom is sterk sigomorf. Die perigoniumsegmente begin op dieselfde hoogte, behalwe by H. abbreviatum waar die drie anterieure segmente laer as die ander aan die perigoniumbuis vas is (Fig. 15C).

Die segmente is korter as die perigoniumbuis en verskil in 'n mindere of meerdere mate van mekaar in vorm en grootte. By *H. watsonium* en *H. priorii* is die segmente van 'n blom byna ewe lank, maar by die ander is daar heelwat verskil in lengte en breedte. Die grootste verskil kom voor by *H. abbreviatum* waar die drie anterieure segmente verskeie male kleiner is as die ander segmente (Fig. 15C). Hierdie spesie kan as die laaste stadium van die progressiewe perigoniumheterofillie beskou word. Op grond van hierdie kenmerk het N. E. Brown (1932) besluit om dié spesie apart in Salisbury se destyds nog onbeskryfde genus *Petamenes* te plaas wat, volgens Brown, gekenmerk is deur "very unequal" perigoniumsegmente, teenoor *Homoglossum* met "subequal or not very unequal" segmente. Lewis (volgens 'n ongepubliseerde nota in BOL) en Goldblatt (1971) meen egter dat die afskeiding van *H. abbreviatum* in 'n aparte genus, nie geregverdig is nie.

Die posterieure segment (in hierdie werk soms ook genoem die topsegment) wat aan die binnekrans van blomdekblare behoort, is die grootste. Dit is reguit vooruitgestrek, dikwels effens konkaaf en vorm 'n kap oor die helmknoppe en stempels. Die twee segmente weerskante daarvan (ook genoem die top-laterale of posterieur-laterale) is effens of heelwat kleiner. Die drie anterieure segmente is meestal nog kleiner, met die onder-mediane of anterieure segment dikwels effens korter (H. abbreviatum) of langer (bv. H. guthriei, H. muirii) of smaller (H. quadrangulare) as die twee weerskante (onder-laterale of anterieur-laterale). Die laasgenoemde vyf segmente is spreidend (bv. H. huttonii) of teruggebuig (bv. H. quadrangulare, H. watsonium, H. priorii) wat aan die blom 'n slanke vleuelagtige voorkoms gee. By H. merianellum is die groep segmente koppievormig met die rande van die segmente oorvleuelend.

Die blomkleur is rooi of rooipienk, soms oranje, geel of appelkooskleurig. Dit word by die spesiesbeskrywings aangedui met RHS-nommers van die Royal Horticultural Society se kleurkaarte. Marloth (1915) vind dat die kleur by *H. merianellum* te wyte is aan 'n mengsel van twee pigmente in die perigonium-epi-

dermis: rooi selsap en 'n laag geel korrels in die basis van die epidermisselle, d.w.s. antosianien en chromoplaste. Hy vermeld verder dat as die rooi pigment afwesig is, is die blomme suiwer geel.

Die blomme is geurloos. Hulle bly ongeveer vier dae oop.

Die drie nektarkliere is, soos tipies van die Ixieae, septaal in die top van die vrugbeginsel geleë (Fig. 3D). Die nektar word deur drie smal kanaaltjies in die basis van die perigoniumbuis gestort vanwaar dit met kapillariteit opstyg tot in die nektar-versamelsakkie. Volgens Vogel (1954) word *H. merianellum* deur voëls bestuif.

Die androecium—Die meeldrade van die tien spesies is so eenders dat hulle omtrent geen diagnostiese kenmerke verskaf om die spesies te onderskei nie. Die helmdrade is lank, tereet, naak en ingeplant in die perigoniumbuis waar dit skielik verbreed, met die anterieure helmdraad ongeveer 5 mm laer ingeplant as die ander twee (Fig. 3A).

Die helmknoppe besit parallelle thecae (Fig. 3F) en staan eksentries, ewe hoog in 'n ry langs mekaar teen die posterieure segment, met die thecae na die anterieure kant gewend (Fig. 3A). Die helmknoppe is een-kwart tot een-derde vanaf hul basisse, en by *H. huttonii* byna by hul middelpunt, aan die helmdrade geheg; onder die aanhegtingspunt is hulle pylpuntvormig, met die thecae vry van mekaar en skerppuntig (Fig. 3F). Aan hul toppe is die helmknoppe taamlik stomp of soms ingekeep en is daar dikwels 'n klein uitbreiding van die helmbindsel wat die top klein-apikulaat maak. Hul toppe reik gewoonlik nie tot die top van die posterieure segment nie, behalwe soms by *H. quadrangulare*, *H. vandermerwei* en *H. abbreviatum*.

Die pollen is monokolpaat en die seksien punktitegillaat, met 'n onreëlmatige, taamlik vlak, verrukoiede skulptuur op die tegillum.

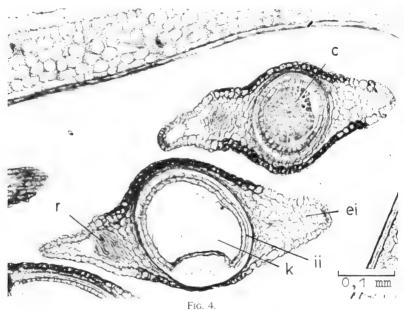
Die gynoecium verskaf ook omtrent geen diagnostiese kenmerke nie. Die driehokkige vrugbeginsel met sy talryke, asstandige saadknoppe, is 5–6 mm lank. Die styl is 4,5–8 cm lank en het drie kort styltakke tot 5 mm lank.

Die drie stempels is ongeveer soos by *Gladiolus:* wanneer die blom open, is hulle konduplikaat; later word hulle dikwels oopgevou en hartvormig, of soms bly hulle min of meer skeef-tregtervormig en gekeep (Fig. 3C). Die reseptiewe gedeelte van die stempel bestaan uit klein papille op hul boonste rande. Die stempels verskil in breedte: by die meeste spesies ongeveer 2 mm breed in hul oopgevoude toestand; by *H. guthriei, H. huttonii* en *H. watsonium* is hulle tot 4 mm breed; by *H. vandermerwei* skaars 1 mm breed en tot 3 mm lank, met die papille ook op die syrande, tot naby die basisse van die styltakke.

Die doosvrugte, nog omgewe deur die uitgedroogde bractea en bracteola, is van 2 tot 4,5 cm lank en het 'n effens verharde, taamlik dun, membraanagtige perikarp met 'n effens bulterige oppervlakte. Hulle is hokspletig en later splits die sentrale as ook in drie dele, sodat daar drie spreidende kleppe is.

Die sade is skyfvormig, met 'n ongeveer 1 mm breë, dun membraanagtige

vleuel rondom, wat 'n ontwikkeling van die rafe en die buitenste integument is (Fig. 4) en wat later uit groot, sagte, luggevulde dooie selle bestaan met heelwat intersellulêre ruimtes tussenin. Geen wesenlike verskil kon tussen die sade van *Homoglossum* en die Suid-Afrikaanse *Gladiolus*-spesies wat vir ondersoek beskikbaar was, opgemerk word nie.



Homoglossum watsonium, dwarssnee deur vrugbeginselhok ná bevrugting, met twee saadknoppe: c, chalaza; ei, buite-integument; ii, binne-integument; k, kiemsak; r, rafevaatbundel.

ANATOMIESE ONDERSOEK

Materiaal en metode—Vars materiaal van al die spesies behalwe van H. fourcadei is uit die veld versamel vir die anatomiese en sitologiese ondersoek.

Dwarssneë is vryhand, met 'n vriesmikrotoom en met 'n rotasiemikrotoom gemaak deur die laminas van die basale loofblare op hul middelhoogte. Die sneë is gekleur met saffranien en Delafied se hematoksilien en permanent gemaak, of gekleur met Delafied se hematoksilien en Sudan III en in gliserienjellie gemonteer vir die aanwys van die kutikula. Blaarstukkies is met Jeffrey se vloeistof gemasereer om die xileemelemente te ondersoek.

Stukkies van die knoltunicae is met die vriesmikrotoom gesny, asook met Jeffrey se vloeistof gemasereer en met saffranien gekleur.

Die knoltunicae-In hul anatomiese bou verskil die harde knoltunica van die

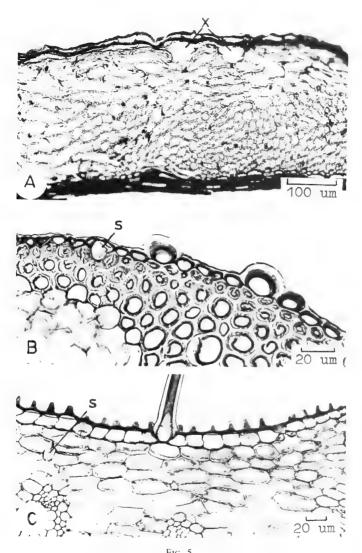


FIG. 5.

Homoglossum, dwarssneë deur blare: A, knoltunica, H. watsonium; B, epidermis en subepidermale sklerenchiem, kostale streek, H. huttonii; C, interkostale streek, H. merianellum; s, styloïed in dwarssnee; x, kristal.

twee spesies van die seksie *Homoglossum* heelwat van die sagter tunicae wat by die ander seksies aangetref word.

By *H. abbreviatum* en *H. quadrangulare* waar sagte membraanagtige tunicae voorkom, is slegs die kostale sones van die tunica gelignifiseer, terwyl die interkostale sones parenchimaties bly. In die onderste helfte van die tunica bestaan die kostale sones uit parallelle veselstringe wat van mekaar losskeur om die smal knolfibrille te vorm wat kenmerkend is van hierdie spesies. In die boonste helfte van die tunica vorm die veselstringe 'n netwerk wat verhoed dat die tunica verder ingeskeur word. Die onverhoute parenchiem in die mase van die netwerk word droog maar verdwyn nie.

By die seksie *Homoglossum* verander die parenchimatiese interkostale dele van die tunica tot gelignifiseerde parenchiem en sklereïede van verskillende vorms, sommige met besonder dik selwande en stippels met lang stippelkanale. Ook kom intermediêre vorms voor tussen sklereïede en vesels. In die boonste helfte van die tunica kom 'n kontinue laag van hierdie seltipes onder die uitgedroogde abaksiale (buitenste) epidermis voor (Fig. 5A). Wanneer die epidermis verwyder is, is daar met 'n lens klein verspreide holtetjies (foveolae) sigbaar, in elk waarvan 'n groot kubieke kristal in 'n dunwandige sel lê. Soms kom van hierdie kristal-idioblaste ook dieper voor. Die kostale dele bestaan uit veselbundels wat oorlangs loop. In die onderste helfte van die tunica bly die interkostale stroke onverhout of min verhout. Hierin ontstaan die splete waardeur die tunica in die kenmerkende breë slippe geskeur word. Elke slip bestaan uit breë veselstringe met 'n klein hoeveelheid verhoute parenchiem en sklereïede daarby.

Die loofblare—Die epidermisselle op die kostale en interkostale sones verskil in grootte en selwanddikte: oor die sklerenchiemribbe (kostale sones) is hulle meestal klein en taamlik sklerenchimaties, met klein lumina, dik selwande en 'n dik kutikula. Die klein dikwandige haarstompies wat by sommige spesies op die rande van die sklerenchiemstroke voorkom, is uitgestulpte epidermisselle. Ook is daar dikwels rye groter koepelvormig uitgestulpte selle op die kostale sones by sommige spesies aanwesig (Fig. 5B). Hulle is tot nagenoeg tweemaal hoër en breër as die omliggende epidermisselle en is waarskynlik homoloog met die haarstompies.

Die epidermisselle van die interkostale sones is tot viermaal breër en hoër as dié van die kostale sones, bv. by H. quadrangulare. Die sellulose- en pektienbevattende buitewande onder die kutikula is $4~\mu m$ tot soms $10~\mu m$ dik, terwyl die kutikula self slegs tot $1~\mu m$ dik is. Die antiklinale en binne-periklinale selwande is meestal dun

By *H. merianellum* is sommige interkostale epidermisselle verleng en uitgestulp om lang, eensellige trichome te vorm wat met 'n dik kutikula bedek is (Fig. 5C).

By die meeste spesies kom 'n ry van vier tot agt papille voor op elke interkostale epidermissel, soortgelyk aan dié by sommige *Romulea*-spesies (de Vos, 1970). Hulle is soliede verdikkings van die buitenste sellulose- en pektiensel-

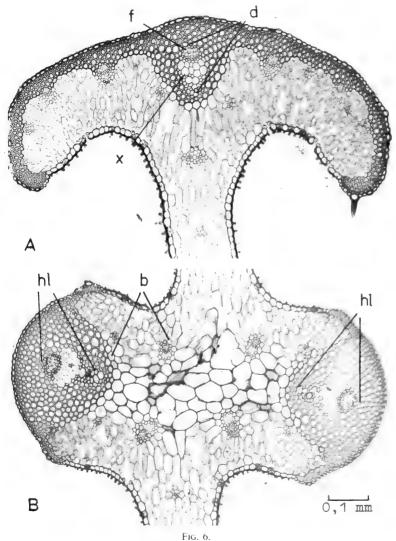


Fig. 6.

Homoglossum watsonium, dwarssnee deur loofblaar: A, verbrede blaarrand; B, pseudomiddelaar-gedeelte; b, bundelskede; d, dorsale mediane vaatbundel; f, floëem; hl, hooflaterale vaatbundel; x, xileem.

wandlaag (Fig. 5C) en is bedek met die dun kutikula. By verskeie spesies, bv. H. merianellum, is hulle 7–10 μ m hoog en is selfs in herbariumeksemplare sigbaar met 'n 50-maal vergrotende lens. By H. vandermerwei en H. muirii is daar meestal slegs spore daarvan te sien en by H. priorii is hulle afwesig.

Die stomata is ingesink (Fig. 5C), sonder hulpselle, en kom slegs interkostaal voor, taamlik reëlmatig versprei tussen elke tweede tot vierde of vyfde epidermissel.

Die mesofil bestaan grotendeels uit chlorenchiem wat in die interkostale sones subepidermaal geleë is en in die kostale sones dieper onder die sklerenchiemlaag lê. By *H. priorii* is die weefsel uitgesproke palissadevormig. By die ander spesies is die selle parallel met die blaaroppervlak verleng, behalwe in die verbrede blaarrande van *H. watsonium* (Fig. 6A) waar die verlengde selle palissadevormig of skuins tot die epidermis geplaas is. Intersellulêre ruimtes in die chlorenchiem is klein en min. Groot kleurlose parenchiemselle kom tussen die twee hooflaterale are by *H. watsonium* en *H. vandermerwei* voor, en in die sentrale gedeelte van die vier-vleuelige blare.

Daar is geen tannien-bevattende idioblaste in die blare nie. Al die spesies besit groot suilvormige styloïede, $125-150~\mu m$ lank en vierkantig in dwarssnee (Fig. 5B, C), soortgelyk aan dié by *Romulea* (de Vos, 1970) en *Syringodea* (de Vos, 1974). Hulle kom subepidermaal voor (*H. merianellum*, *H. priorii*), of soms skynbaar epidermaal (*H. watsonium*), in rye in die kostale sones, asook enkel versprei diep in die mesofil.

'n Groot aantal parallelle vaatbundels kom voor met min dwarsverbindings. Al die groot are, bv. die mediane dorsale en ventrale vaatbundels wat onderskeidelik in die abaksiale en adaksiale rande van die unifasiale blaar lê, en die hooflaterale bundels, is ingebed in 'n massa sklerenchiemvesels wat in gemasereerde preparate geblyk het 0,5 tot 1,2 mm lank te wees. Die talle klein are, diep in die mesofil geleë, is dikwels sonder sklerenchiem. Soos by unifasiale blare te verwagte, lê die vaatbundels met hul floëem na die epidermis gekeer en die xileem na binne (Fig. 6A, B).

Die mediane dorsale en ventrale vaatbundels met hul sklerenchiemskedes is eenders by die ondersoekte soorte, behalwe by *H. priorii* waar die twee ventrale bundels in die adaksiale rand nie versmelt is nie (Fig. 2A).

By die vier-vleuelige blare van bv. *H. quadrangulare*, asook by die byna terete blaar van *H. muirii*, is al vier die rande eenders, verbreed met 'n breë laag subepidermale sklerenchiem, en met een groot vaatbundel en 'n aantal kleineres weerskante van die grote (Fig. 2F, G). By die *H. watsonium*-blaar is die sklerenchiemriwwe van die hooflaterale are smaller as dié van die dorsale en ventrale rande en is daar slegs 'n enkele klein aar weerskante van die hooflaterale aar. Die rif van die laasgenoemde aar lê opgehewe in die middel van die lamina-oppervlakte en lyk na 'n sterk ''middelaar'' (Fig. 2E)—die ''pseudomittelrippe'' van Napp-Zinn (1974).

By die groot bundels is die parenchimatiese bundelskedes onderbroke en slegs hier en daar onderskeibaar—waarskynlik is hulle gedeeltelik vervang deur vesels. Die klein inwendige bundels het vollediger bundelskedes.

Die vaatbundels stem grootliks ooreen met Cheadle en Uhl (1948a) se monokotiel Tipe I bundel, waarby die grotere metaxileemelemente ongeveer ewe groot is en die xileem en floëem in 'n reguit of geboë lyn ontmoet (Fig. 6). Die tracheïede van die metaxileem is hoofsaaklik leertracheïede. Die protoxileem, wat nie by al die vaatbundels voorkom nie, bevat hoofsaaklik spiraaltracheïede. In gemasereerde weefsel gemeet, is die tracheïede 500 μ m of langer. Tracheae kom nie voor nie.

Die metafloëem bevat verskeie sifbuise en heelwat begeleidende selle wat effens onreëlmatig gerangskik is (Fig. 6), en min of meer ooreenstem met Cheadle en Uhl (1948b) se Intermediêre monokotiel-floëemtipe. Rondom is 'n lagie floëemparenchiem. Geöblitereerde oorblyfsels van die protofloëem is veral in die hooflaterale bundels waarneembaar.

Nie net morfologies nie, maar ook anatomies stem die blare van *Homoglossum* ooreen met die *Gladiolus*-spesies van die groep *Unifoliati* wat vir vergelyking ondersoek is, onder andere in die ingesinkte stomata sonder hulpselle, die aanwesigheid van styloïede, haarstompies en groter epidermisselle op die kostale sones, in die bou van die vaatbundels en in die afwesigheid van tannien.

CHROMOSOOMONDERSOEK

Voorheen is die chromosome van vier *Homoglossum*-spesies ondersoek deur Bamford (1941), Sharma en Talukdar (1960) en Goldblatt (1971). Die huidige ondersoek van nog drie spesies bring die totaal van die ondersoekte spesies op sewe te staan (Tabel 1). Twee van die reeds ondersoekte spesies se chromosoomtellings is nou geverifiëer.

Metode—Bywortels verkry van knolle wat in April op klam sand gespruit het, is in asynsuur-alkohol gefikseer na 'n voorbehandeling met 0,001 M 8-hidroksikinolien, of met 'n versadigde paradichlorobensienoplossing. Daarna is die wortelpunte gekleur ôf met karmynasynsuur vir 24 uur, ôf met laktopropioonorseïen (Dyer, 1963), wat effens beter resultate opgelewer het as die eersgenoemdes. Tydelike platgepersde preparate in 45 persent asynsuur is daarvan gemaak.

Resultate —Al die ondersoekte spesies het 'n diploïede chromosoomgetal van 30 (Tabel 1), behalwe vir drie gekweekte vorms van Gladiolus watsonius wat volgens Sharma en Talukdar (1960) 2n = 66 het. Moontlik was hier 'n verkeerde identifikasie.

Die chromosome is klein, byna uniform in grootte (Fig. 7), met submediane sentromere (volgens Goldblatt is hulle akrosentries). Hul lengtes lê tussen 1 en 2 μ m. Daar kon nie tussen die kariotipes van die verskillende spesies onderskei word nie. Die kariotipes stem grootliks ooreen met dié van *Gladiolus*, enkele

spesies waarvan nou weer ondersoek is (vgl. ook Goldblatt, 1971). Dit dui ook op die noue verwantskap tussen die twee genera.

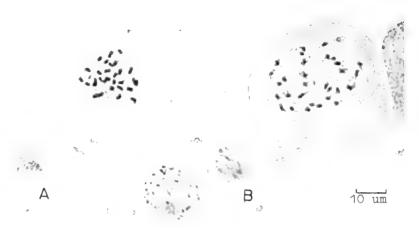


Fig. 7.

Chromosome in wortelpuntmitoses: A, *Homoglossum watsonium*, metafase; B, *H. abbreviatum*, laat-profase.

GEOGRAFIESE VERSPREIDING

Homoglossum kom in die suid-westelike winterreënstreek en die aangrensende distrikte van die Kaap-provinsie voor, asook in die suidkusdistrikte wat hul reën deur die jaar ontvang. Die genus beslaan 'n lang smal strook van ongeveer 200 by

TABEL 1. Chromosoomgetalle van *Homoglossum-*spesies

Spesie	De Vos- Versamelno.	Diploïde chrgetal		Verwysing
H. priorii		30	Kaapse Skiereiland	Goldblatt 1971
H. merianellum		30	Kaapse Skiereiland	Goldblatt 1971
H. merianellum var. aureum	2302	30	Kaapse Skiereiland	
H. watsonium	2383	30	Stellenbosch	ł
H. watsonium	2287	30	Tulbagh	
H. watsonium		30	Kaapse Skiereiland	Goldblatt 1971
H. watsonium		30	*	Bamford 1941
H. watsonium		66		Sharma & Talukdan 1960
H. muirii	74/3	30	Ex hort. Augustyn	
H. quadrangulare	2303	30	Ceres	
H. huttonii	2291	30	Knysna	
H. abbreviatum	2305	30	Heidelberg	
H. abbreviatum		30	Caledon	Goldblatt 1971

Opsomming van die geografiese verspreiding van Homoglossum-spesies in magistraatsdistrikte of distriksgroepe. Spesies

word aangedui deur die eerste letters van die spesiesname.	dui deni	die e	erste le	tters va	in die spesie	sname.				
	Sek	sie Lin	Seksie Linearifolium	ium	Seksie Ho	Seksie Homoglossum	Seksie Quadrangulifolium	Опас	rangul	ifolium
Distrikte	prio.	prio. mer.	guth. vand.	vand.	wats.	muir.	quad.	abbr.	quad. abbr. fourc. hutt.	hutt.
Malmesbury—Hopefield	+				+					
Kaapse Skiereiland	+	+			+					
Somerset-West—Stellenbosch—Paarl	+	+			+					
Tulbagh—Ceres					+		+			
WorcesterMontagu	+					+	+	+		
Caledon-Hermanus	+		+			+		+		
Вгедаздогр	+		+	+		+		+		
Swellendam—Heidelberg				+		+		+		
Riversdale—Mosselbaai						+		+		
Клуsna—Нитапзdогр									+	+
Klein-Karoo									+	
Port Elizabeth—Grahamstad—Oos-Londen										+

1 000 km vanaf Saldanhabaai tot Oos-Londen, tussen die suiderbreedtegrade 33° en 34°50′ en die oosterlengtegrade 18° en 28°. 'n Paar spesies van Sentraal-Afrika is ook as *Homoglossum* beskryf, maar dit is moontlik dat hulle beter by *Gladiolus* tuishoort, weens hul perigoniumbuise wat, hoewel lank, nie duidelik in twee aparte, konstante wydtes met 'n skielike oorgang tussenin, onderskei kan word nie.

In Suid-Afrika kom die spesies voor vanaf die seevlak (H. priorii) tot 1 000–2 000 meter bo seespieël (H. quadrangulare). Sommige staan langs paaie (H. watsonium, H. muirii, H. abbreviatum), ander op kalkkliprandjies (H. guthriei), op klam, suur sandgrond (H. merianellum) of op kleigrond en braaklande (H. watsonium).

Volgens die jongste geologiese kaart van die Republiek blyk dit dat die spesies veral op die strata van die Kaapse sisteem en op Malmesbury-lae voorkom, asook op resente ongekonsolideerde afsetsels van kalk, sandsteen en gruis; ook dat sommige spesies hoofsaaklik op sekere lae voorkom, maar tog dikwels op ander naby geleë lae gekry is. H. merianellum groei hoofsaaklik op Tafelbergsandsteen; H. watsonium hoofsaaklik op Malmesbury-skalie, H. muirii en H. quadrangulare op Bokkeveldlae van die Kaapse sisteem; H. guthriei, H. vandermerwei, H. fourcadei en H. abbreviatum veral op Tafelbergsandsteen en Bokkeveldlae en die eersgenoemde ook op resente lae.

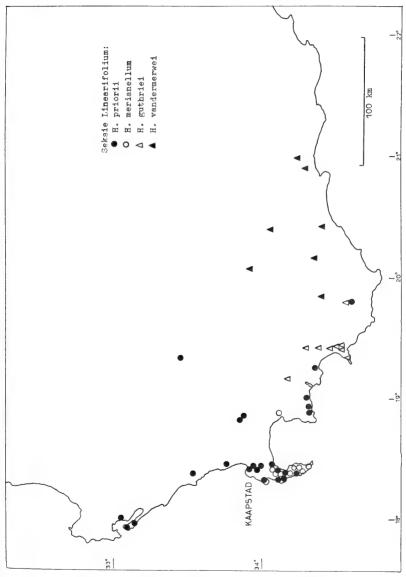
Die twee spesies met die wydste verspreiding kom voor op verskeie geologiese strata: *H. priorii* wat vanaf Saldanhabaai tot die Kaapse Skiereiland en die suidkusdistrikte van Caledon en Bredasdorp versprei is en dikwels naby die see voorkom, staan op Malmesburylae, Tafelbergsandsteen en resente afsetsels.

H. huttonii, met 'n verspreiding van Knysna tot Grahamstad en met een opgawe van naby Oos-Londen, kom voor op Tafelbergsandsteen, Bokkeveld, resent, en in die Albany-distrik moontlik op Witteberg- en Dwykalae.

Enkele spesies het besonder klein areale, t.w. *H. merianellum* wat, behalwe vir twee twyfelagtige opgawes, slegs in die suidelike helfte van die Kaapse Skiereiland voorkom, 'n area van minder as 40 km by 10 km; en *H. guthriei* wat, sover bekend, slegs in die Caledon-Bredasdorp-distrikte oor 'n afstand van skaars 40 km aangetref word.

In Tabel 2 word 'n opsomming gegee van die verspreiding van die seksies met hul spesies, vir die magistraatsdistrikte of distriksgroepe gerangskik vanaf die noordweste na die suidooste. Daaruit blyk dat die Bredasdorp-distrik die meeste spesies het. Die seksie *Linearifolium* kom merendeels voor in die suidwestelike hoek van Kaapland met *H. priorii*, wat moontlik die primitiefste spesie is, die wydste versprei (Fig. 8). Die ander drie spesies van die seksie het klein areale, met dié van *H. guthriei* en *H. vandermerwei* gedeeltelik oorvleuelend.

Die seksie *Homoglossum* het byna dieselfde verspreiding as die seksie *Linearifolium*. Sy twee spesies kan as vikariante beskou word met naastenby aangrensende areale (Fig. 9). Die derde seksie, *Quadrangulifolium*, kom merendeels in die suide



 $\label{eq:Fig. 8.} \textit{Fig. 8.}$ Geografiese verspreiding van Homoglossum, seksie Linearifolium.

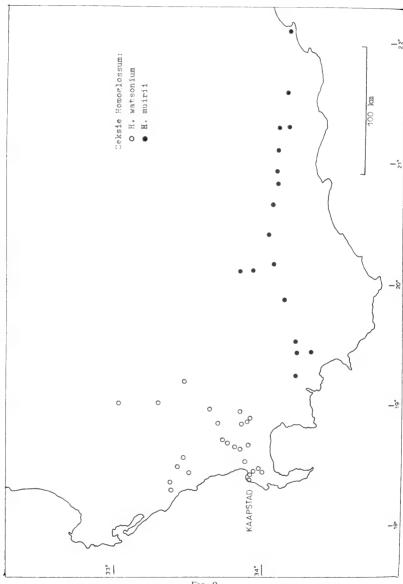
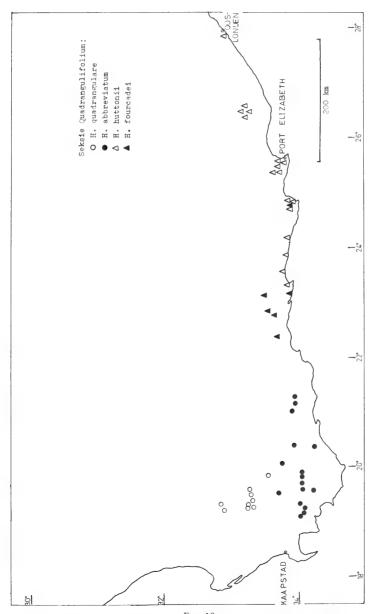


Fig. 9.
Geografiese verspreiding van *Homoglossum* seksie *Homoglossum*.



 $\label{eq:Fig. 10.} Fig.~10.$ Geografiese verspreiding van Homoglossum,seksie Quadrangulifolium.

voor (Fig. 10). *H. quadrangulare* het 'n konsentrasiesentrum in die Ceres-distrik. *H. huttonii* en *H. fourcadei* wat naverwant is, is hoofsaaklik beperk tot die suidkusdistrikte vanaf Knysna ooswaarts, met die laasgenoemde ook in die Klein-Karoo. Die areaal van *H. abbreviatum* lê tussen dié van *H. quadrangulare* en die *huttonii-fourcadei*-groep.

GESKIEDENIS

Geen pre-Linnaeïese tekening of beskrywing van 'n Homoglossum kon opgespoor word nie en in die Species Plantarum van 1753, asook dié van 1762 word geen spesie genoem wat moontlik 'n Homoglossum kan wees nie. Skynbaar is homoglossums eers vanaf 1760 in Europa bekend, toe Johannes Burman in 'n brief aan Linnaeus 'n nuwe Antholyza-spesie aankondig wat by hom blom en waarvan hy 'n blom in sy brief insluit. Die blom is nog steeds in Burman se brief te sien, volgens 'n persoonlike mededeling van prof. T. T. Barnard wat 'n studie maak van die korrespondensie in die Linnaeus-versameling in Londen tussen Linnaeus, die Burmans en David van Royen. In sy antwoord aan Burman het Linnaeus die plant geïdentifiseer as Gladiolus tristis. Drie jaar later gee D. van Royen in sy manuskrip, Centuria observationum et quaestionum botanicarum, 'n breedvoerige beskrywing van dieselfde spesie onder Antholyza? capensis. Dit het toe by hom geblom, moontlik uit 'n besending wat hy ôf direk van die Kaap ôf van Burman ontvang het. In die kantlyn van hierdie manuskrip het Linnaeus aangeteken: Anthol. aethiopica; en op die eksemplaar LINN 60.4, wat baie goed ooreenstem met Van Royen se beskrywing en wat waarskynlik Van Royen se plant is, het Linnaeus dieselfde identifikasie gemaak. Linnaeus het dus hierdie spesie (nou H. quadrangulare) tweemaal verkeerd geïdentifiseer (volgens Barnard, persoonlike mededeling).

In 1768 beskryf die jonger Burman die spesie as *Antholyza quadrangularis* en voeg by: "1760 Majo mense florit apud nos". Die tipe daarvan is in die Burman-herbarium in Genève.

Die tweede *Homoglossum*-spesie wat in Europa bekend geraak het, was *H. merianellum* wat Linnaeus in 1774 (Syst. Veg. ed. 13) beskryf onder *Antholyza merianella* en verkeerdelik as dieselfde as Miller se plant (Ic. 297 fig. 2, 1760) beskou, wat 'n *Watsonia* is. Daar Miller se plant egter reeds in 1768 beskryf is as *W. humilis* Mill., was Linnaeus se naam daarvoor oorbodig en illegitiem. In 1784 beskryf Thunberg 'n soortgelyke *Homoglossum* wat hy op sy Kaapse reise versamel het, as *Gladiolus merianellus*, sonder die sitasie van òf Miller òf Linnaeus se plant as sinonieme.

Volgens Milne-Redhead (1938) kan hieruit afgelei word dat Thunberg besef het dat Linnaeus die plant verkeerdelik as dieselfde as Miller se plant beskou het: die naam vir dié homoglossum dateer dus van 1784 en moet aan Thunberg toegeskryf word.

Die derde Homoglossum is in 1780 deur Houttuyn geteken onder die verkeerde

naam *Gladiolus recurvus* L. Hierdie plant, wat in die Burman-herbarium bewaar word, het N. E. Brown (1929) beskou as 'n nuwe spesie, *Antholyza acuminata*, wat hy in 1932 na *Homoglossum* oorplaas. Dieselfde spesie is 'n paar jaar later deur Jacquin beter geteken (Ic. 239) en beskryf as *G. watsonius* Jacq. (1789), en in 1797 is dit deur Andrews geteken onder die naam *G. praecox* var. *flore rubro*.

In die negentiende eeu is *Homoglossum*-spesies meer as eenmaal verwar. Ker (1802) by voorbeeld, beskou 'n plant met baie klein anterieure perigoniumsegmente en groot posterieure segmente, wat Andrews (1801) as *G. abbreviatus* beskryf het, as dieselfde as die jonger Burman se *Antholyza quadrangularis*, moontlik omdat die blare van die twee spesies eenders is; hy noem sy plant *Gladiolus quadrangularis* en siteer *G. abbreviatus* Andr. as 'n sinoniem. Die werkers ná Ker, onder andere Baker (1896), beskou ook die twee spesies as eenders, tot N. E. Brown (1932) die saak regstel deur *H. abbreviatum* sy ou geldige epiteton terug te besorg, maar onder die genus *Petamenes*.

N. L. Burman (1768) gee 'n kort beskrywing van Antholyza revoluta wat, vermeld hy, in 1757 in die maand Oktober geblom het. In 1929 kon Brown geen tipe hiervan in die Burman-herbarium vind nie; hy beskou dit as 'n twyfelagtige spesie, ook weens die kort, niks beduidende beskrywing daarvan. Poiret (1812) egter gee A. revoluta Burm. aan as 'n sinoniem vir die homoglossum Gladiolus watsonius Jacq. (1789). Daarop aanvaar Baker goedertrou die epiteton revolutus vir G. watsonius: in 1877 as Homoglossum revolutum, in 1892 as G. revolutus, en in 1896 as Antholyza revoluta Burm. Van toe af is H. watsonium by die Suid-Afrikaanse botaniste onder die epiteton revolutum bekend, totdat Brown (1929, 1932) die twyfelagtigheid van hierdie naam aantoon.

H. Bolus en Wolley-Dod (1903) ontdek dat daar onder Baker se A. revoluta Burm. twee aparte spesies is wat hulle as G. watsonius Thunb. en A. revoluta Burm. bestempel. Maar N. E. Brown (1929) met sy studie van die Burman-plante, kon aantoon dat die bogenoemde A. revoluta van Bolus en Wolley-Dod die egte G. watsonius Thunb. is, en dat hul G. watsonius anders is as Thunberg se plant en nog sonder 'n wettige naam is. Brown beskryf dit daarop as Antholyza priorii en plaas dit in 1932 in die genus Homoglossum.

Uit die bostaande blyk dat die *Homoglossum*-spesies in die vorige eeue onder die genera *Gladiolus* en *Antholyza* geplaas is. Die genusnaam *Homoglossum* kom van Salisbury (1812) en is gebaseer, sonder 'n genusbeskrywing, op die plant wat Andrews (1797) geïllustreer en beskryf het as *G. praecox*. Salisbury het die naam *Homoglossum* gekies weens die byna ewe groot perigoniumsegmente daarvan. In 1866 gee hy 'n onvolledige beskrywing van die genus. In 1877 is dié genusnaam deur Baker aanvaar; maar in 1892 maak Baker dit 'n subgenus van *Gladiolus* en in 1896 laat vaar hy dit en plaas die *Homoglossum*-spesies terug onder *Antholyza*.

Bentham en Hooker (1883) noem die genus *Homoglossum* in klein hoofletters aan die einde van die Iridaceae net ná die genus *Antholyza*, met 'n aantekening daarby dat dit apart van *Antholyza* is weens sy minder ongelyke (''minus

inaequales'') perigoniumsegmente. Pax (1888) plaas drie *Homoglossum*-spesies onder *Antholyza* met die aantekening dat die perigoniumsegmente nie veel verskil nie, en Diels (1930) maak *Homoglossum* 'n seksie van *Antholyza*.

In sy reeds genoemde werk van 1932 vind Brown dat die genus *Antholyza*, soos dit toe beskou is, uit verskeie nie-eenderse struktuurtipes bestaan, nie een waarvan ooreenstem met die genuskenmerke soos Linnaeus dit in die eerste tot vyfde uitgawes van die *Genera Plantarum* beskryf het nie (1737–1754). Brown verdeel daarop die spesies wat vanaf Ker se tyd verkeerdelik onder *Antholyza* gereken is, in agt genera, ''all of which have good distinctive and easily recognized characters''. Een van die genera is *Homoglossum* Salisb., gekenmerk onder andere deur los are met die buitenste skutblaar groter as die binneste, blomme met 'n gebuigde perigoniumbuis wat naby of onder die middel vernou tot 'n smal basale gedeelte, en breë segmente—wat ''subequal or not very unequal'' is, maar met die dorsale een taamlik groter as die ander. Daaronder plaas hy elf spesies van Suid-Afrika en twee van Sentraal-Afrika.

Een van die elf spesies wat Brown noem, *H. caryophyllaceum*, is deur Lewis *e.a.* (1972) na *Gladiolus* verplaas. In die huidige werk word getoon dat drie spesies, te wete *H. acuminatum*, *H. flexicaule* en *H. gawleri* konspesifiek is met *H. watsonium*. Daar bly dus sewe goeie spesies van die wat Brown noem, oor.

In sy 1932-publikasie stel Brown ook weer die genus *Petamenes* Salisb. in vir plante met perigoniumblare van "very unequal size", met verskeie spesies van tropiese Afrika en drie van Suid-Afrika. Twee van die laasgenoemde het later geblyk homoglossums te wees, en is daarheen oorgeplaas, t.w. *P. guthriei* (deur L. Bolus, 1933) en *P. abbreviatum* (deur Goldblatt, 1971), die laasgenoemde spesie synde die tipespesie van *Petamenes*.

In 1931 beskryf L. Bolus H. vandermerwei (as Antholyza) en in 1933 H. hollandii wat nou blyk dieselfde te wees as H. huttonii.

In hul *Gladiolus*-monografie verskuif Lewis *e.a.* (1972) die spesie *G. aureus* na *Homoglossum* "for, although the shape of the flower is different, in corm, leaf and seed it so closely resembles *H. merianellum*". Die huidige ondersoek toon egter dat hierdie spesie, weens sy perigoniumbuis wat na bo tregtervormig verbreed, beter in *Gladiolus* tuishoort. Indien dié spesie onder *Homoglossum* moet staan, verval die enigste wesenlike verskil tussen die twee genera, te wete die vorm van die perigoniumbuis.

VERWANTSKAPPE

Die genus *Homoglossum* staan baie na aan *Gladiolus* en verskil slegs in die vorm van die perigoniumbuis wat in die onderste gedeelte smal-buisvormig is en onder sy middel skielik breër word tot 'n breë, min of meer silindriese buis wat byna konstant in breedte bly tot by die segmente. Dit het dikwels 'n klein uitstulping of sakkie na die anterieure kant vir die versameling van die nektar. Die perigoniumbuis van *Gladiolus* daarenteen is tregtervormig en verbreed geleidelik na bo.

Die huidige noukeurige ondersoek van die uitwendige kenmerke van die knol, blare, blomme, vrugte en sade, en die anatomiese ondersoek van die blare, sade en knoltunicae, asook die sitologiese ondersoek van die kariotipe (Goldblatt 1971 en die huidige ondersoek) toon dat die *Homoglossum*-spesies geen ander kenmerke besit wat nie ook by sekere *Gladiolus*-spesies voorkom nie. Die feit dat sommige *Homoglossum*- en *Gladiolus*-spesies maklik verbaster, ook in die veld, toon ook hul nabye verwantskap. Met reg beskou Goldblatt (1971) die genus as 'n "genus of convenience", om te verhoed dat die reeds enorme genus *Gladiolus* nie nog groter word nie. Aangesien *Homoglossum* maklik onderskeibaar is deur sy kenmerkende perigoniumbuis en sy tien spesies klaarblyklik naverwant aan mekaar is, word dit apart gehou, soos talle werkers van die twintigste eeu, onder andere Lewis (1950), Phillips (1951), Hutchinson (1959), Melchior (1964), Levyns (1966), en Lewis *e.a.* (1972) ook gedoen het.

Homoglossum staan naaste aan die groep Unifoliati van Gladiolus (Lewis e.a., 1972) waarmee dit ooreenstem in sy meestal enkele, smal, basale loofblaar en sy twee of soms meer korter stingelblare wat die stingel meestal skedevormig bedek, in sy gewoonlik onvertakte aar en klein knol met tunicae wat ôf veselagtig ôf hard en verhout is. Soos die Unifoliati, kom dit ook hoofsaaklik in die winterreënstreek van suidwes-Kaapland voor en blom dit van Mei tot die einde van die lente.

Van Antholyza, soos dit deur Brown (1932) tot sy oorspronklike definisie herstel is, verskil dit geheel en al.

Die kariotipes van die spesies, met hul besonder klein chromosome en eenderse chromosoomgetalle, lewer geen getuienis om die onderlinge verwantskappe van die spesies aan te toon nie.

Moontlik is die byna eenderse perigoniumsegmente, soos by *H. watsonium* en *H. priorii*, primitief. *H. abbreviatum*, wat die grootste verskille in segmentgroottes toon, kan as die hoogste gespesialiseerd beskou word.

Op grond van hul blaarstruktuur kan die spesies in drie groepe ingedeel word: met (1) plat lineêre blare met verskeie parallelle are; (2) min of meer lineêre blare met sterk opgehewe versterkte "middelaar" en rande; en (3) vier-vleuelige blare. Die spesies met die plat lineêre blare is waarskynlik meer primitief as die ander. Van hulle is *H. priorii*, met sy byna eenderse perigoniumsegmente, dan die primitiefste.

Deur die struktuur van die knoltunicae kan die spesies in twee groepe ingedeel word wat tot 'n mate ooreenstem met die indeling gegrond op die blaarstruktuur: (1) spesies met harde knoltunicae wat gesplits is in harde breë slippe (H. watsonium en H. muirii) en (2) spesies met sagter tunicae gesplits in smal fibrille (die ander agt spesies).

As die bogenoemde kenmerke in ag geneem word, kan die spesies in drie groepe ingedeel word wat hier as seksies beskryf word (sien 317). Seksie *Homoglossum* wat slegs die twee laaste vermelde spesies bevat, het harde breë

knoltunicaslippe en blare met sterk opgehewe ''middelaar'' en rande. Seksie *Linearifolium* het vier spesies met plat lineêre blare en sagter knoltunicae wat in smal fibrille splits. Seksie *Quadrangulifolium*, met vier spesies, besit viervleuelige blare en smal, min of meer sagte tunicafibrille. Die onderlinge grootte van die perigoniumsegmente van die blomme varieer binne elke seksie.

Die eerste twee seksies is grotendeels simpatries (Fig. 8, 9), met die spesies versprei vanaf die suid-westelike kusdistrikte tot Riversdal en Mosselbaai. Die areaal van die seksie *Quadrangulifolium* begin nie so ver wes as die ander nie; een spesie daarvan, *H. huttonii*, is ooswaarts versprei tot by Oos-Londen.

GENUSBESKRYWING

Homoglossum Salisb. in Trans. Hort. Soc. **1:** 325 (1812) nomen absque descriptione, et 1866 p. 143; Baker 1877 p. 161; Bentham & Hooker 1883 p. 710; Pax 1888 pro syn.; Dalla Torre & Harms 1900–1907 sub no. 1312 pro syn.; N. E. Brown 1932 p. 277; L. Bolus 1933 p. 46; Lewis 1950 p. 262 et 1954 p. 110; Phillips 1951 p. 222; Hutchinson 1959 p. 652; Melchior 1964 p. 538; Levyns 1966 p. 91; Goldblatt 1971 pp. 411–440.

Antholyza sensu Baker subgenus Homoglossum (Salisb.) Baker 1896 p. 165. Antholyza sensu Diels sekt. Homoglossum (Salisb.) Diels 1930 p. 495 pro parte. Gladiolus L. subgenus Homoglossum (Salisb.) Baker 1892 p. 226.

Petamenes Salisb. ex N. E. Brown 1932 p. 276.

Typus generis Homoglossum watsonium (Thunb.) N.E.Br.

Geofiete met bywortels vanaf die knolbasis en met jaarliks hernude slanke bogrondse spruite wat in die ongunstige seisoen verdor. Gerokte knol byna bolvormig tot eiervormig met harde verhoute, of dun membraanagtige tunicae wat van onder tot bo die middel gesplits is in breë elsvormige slippe of in fyn filiforme parallelle fibrille, en met 'n kort kragie van regop fibrille rondom die stingelbasis; soms met klein sessiele byknolle by die knolbasis. Stingel dun, lank, haarloos, grotendeels bedek met lang blaarskedes, regop of soms met die rachis effens golwend of horisontaal gebuig. Laagteblare (katafils) 2 of soms 3, stingelomvattend, buisvormig, die eerste membraneus, die ander fyngerib en groen na bo. Loofblare meestal 3 of soms tot 7, disting of effens spirodisting, smal, akuminaat, naak of soms behaard, meestal heterofil; die basale blaar meestal die langste, met 'n lang, stingel-omvattende buisvormige, fyngeribde blaarskede en 'n unifasiale lamina wat òf lineêr is, dikwels met sterk are en rande, òf kruisvormig in dwarssnee met vier vleuels, of pseudotereet met vier smal groewe; die tweede blaar met 'n langer buisvormige skede en 'n korter unifasiale lamina; die hoogste blaar kort, skutblaaragtig, grootliks bifasiaal. Bloeiwyse 'n los terminale aar, soms vertak aan die basis, met 2-8 blomme of soms meer of net één, die blomme meestal eensydig, sessiel (behalwe H. huttonii), elk met 'n 2-kleppige, blywende bloeiskede (bractea en bracteola). Bractea smal-eiervormig, groot, groen of rooigroen, naak, stomp tot skerp of akuminaat; bracteola korter as

die bractea, met 'n breë membraneuse rand, 2-tandig aan die top. Blom sigomorf, lank, na die anterieure kant gebuig, rooi, oranjerooi, soms pienk of geel, eenkleurig of met die anterieure segmente of die keel verskillend van kleur, sonder geur. Perigoniumbuis krom, langer as die segmente, smal buisvormig in die onderste gedeelte, net onder die middel taamlik skielik verbreed tot 'n silindriese boonste gedeelte wat nagenoeg konstant in wydte is; dikwels met 'n nektarversamelsakkie aan die anterieure kant waar die buis verbreed; segmente van byna rond tot byna lineêr, skerp, akuminaat, stomp of apikulaat, soms byna ewe lank maar meestal met die mediane posterieure segment groter as die ander en reguit, vooruitgestrek. konkaaf of gewelf oor die helmknoppe en stempels, die ander segmente dikwels spreidend of teruggebuig. Meeldrade 3, ingeplant waar die blomdekbuis verbreed; helmdrade filiform, met 'n vlak adaksiale groefie, naak, effens gebuig; helmknoppe lineêr, unilateraal, ewe hoog en aangrensend, die thecae parallel, na die anterieure kant gedraai, klein-apikulaat, (behalwe H. quadrangulare), die basale punte skerp, vry onder die vashegtingspunt; pollen liggeel, 1-sulkaat, verrukojed, punktitegillaat. Vrugbeginsel silindries, ellipsoied of smal omgekeerd eiervormig, met talryke afgeplatte, anatrope saadknoppe op asstandige plasentas in elkeen van die drie hokke; styl lank, filiform, effens krom, die drie styltakke kort; stempels 3, konduplikaat, later skeef-tregtervormig, gekeep of nagenoeg oopgevou en omgekeerd hartvormig, papilvormig op die boonste rande. Doosvrugte smal-ellipsoied tot smal-omgekeerd-eiervormig, korter as die blywende bractea, effens verhout, hokspletig met drie spreidende kleppe; sade talryk, skyfvormig, omring met 'n breë membraneuse vleuel, goud- of ligbruin. Chromosoomgetal 2n = 30.

SLEUTEL TOT DIE HOMOGLOSSUM-SPESIES

1. Mediane posterieure perigoniumsegment (topsegment) effens langer tot twee- of driemaal langer as enige anterieure segment.

2. Blare met sagte syagtige hare 1–2 mm lank op die interkostale sones.

2. Blare naak of met klein haarstompies op die rande van die kostale sones.

3. Lamina van die basale loofblaar lineêr, plat in dwarssnee met verskeie lengte-are, of soms met sterk opgehewe ''middelaar'' en rande, of soms pseudotereet met smal groewe.

4. Knoltunicae membraneus (soms effens verhard), gesplits vanaf die basis van die knol tot bo die middel in fyn fibrille minder as 1 mm breed, die tunicae in die boonste gedeelte meestal ongesplits, met 'n fyn, opgehewe arenetwerk; loofblare dikwels meer as drie (die boonste skutblaaragtig).

5. Bloeiwyse onvertak; die drie anterieure perigoniumsegmente ellipties tot smal-omgekeerd-eiervormig, smal-eiervormig of nagenoeg rond, van ongeveer dieselfde vorm, maar soms kleiner as die posterieure segmente of selde tot die helfte so smal soos die laterale posterieure segmente.

6. Anterieure perigoniumsegmente akuminaat of skerp, smalomgekeerd-eiervormig of smal-eiervormig tot soms eiervormig, byna net so groot en van dieselfde rooi kleur as die posterieure

- 5. Bloeiwyse dikwels vertak; die drie anterieure perigoniumsegmente nagenoeg lineêr, een-derde, of nog minder, van die breedte van die laterale posterieure segmente. 4. H. vandermerwe
- laterale posterieure segmente. 4. H. vandermerwei 4. Knoltunicae verhout en hard, gesplits vanaf die basis van die knol in harde, platterige, subulate slippe wat op hul wydste meer as 1 mm breed is, die tunicae in die boonste gedeelte ongesplits en taamlik glad; loofblare drie (die boonste skutblaaragtig).

 - 7. Perigoniumsegmente minder as tweemaal tot soms tweemaal langer as breed; basale loofblaar filiform of effens afgeplat-silindries maar smal, met vier ewe breë ribbe en vier smal groewe. 6. **H. muirii**
- Lamina van die basale loofblaar lank en smal, kruisvormig in dwarssnee met vier ewe breë vleuels, en ewe breë, sterk ribbe op die rande van die vleuels.
 - Breë boonste gedeelte van die perigoniumbuis ongeveer so lank soos die mediane posterieure segment.
 - Perigoniumbuis met 'n nektarsakkie aan die anterieure kant waar die buis verbreed; sonder lang donkerrooi lengtestrepe op die breë gedeelte van die buis; van die Ceres-distrik 7. H. quadrangulare
 - Perigoniumbuis sonder 'n duidelike nektarsakkie aan die anterieure kant, met lang donkerrooi lengtestrepe op die breë gedeelte van die buis onder die sinusse van die laterale posterieure segmente; van Knysna tot Grahamstad en verder oos. 8. H. huttonii
- Mediane posterieure (top-) perigoniumsegment meer as vyfmaal langer as die mediane anterieure (onderste) segment.
 10. H. abbreviatum

1. SEKSIE LINEARIFOLIUM De Vos sect. nov.

Folium basilare lineare. Tunicae cormi in fibrillis filiformibus e basi fissae.

Typus sectionis: H. merianellum (Thunb.) Baker.

Die vier spesies van die seksie word gekenmerk deur knoltunicae wat vanaf die knolbasis tot ongeveer die middel splits in smal fibrille minder as 1 mm breed, en deur 'n unifasiale basale loofblaar met 'n plat, lineêre lamina met een of meer smal parallelle are en smal versterkte rande. By drie van die vier spesies kom dikwels meer as drie loofblare voor, die boonste korter loofblare bygereken.

Anatomiese verskille kom voor in die blaarstruktuur by die spesies (Fig. 2A-D). By *H. merianellum* en *H. vandermerwei* is die dorsale en ventrale rande van die unifasiale laminas eenders en versterk met 'n sklerenchiembundel so breed soos die lamina, met een aar daarin geleë. By *H. priorii* en *H. guthriei* verskil die dorsale rand van die ventrale. Verder het *H. priorii* min sklerenchiem op die rande. By *H. vandermerwei* is daar, behalwe vir die groot dorsale en ventrale are, meestal slegs twee verdere groot are, t.w. die twee hooflaterale wat regoor mekaar in die middellyn van die lamina lê. Die ander spesies het meer groot are.

H. merianellum is die enigste Homoglossum-spesie met behaarde blare. Op die kostale streke kom by H. guthriei egter haarstompies voor en by H. priori en H. vandermerwei vergrote koepelvormige epidermisselle wat dikwels in rye lê en moontlik homoloog is met die haarstompies van H. guthriei.

Die epidermale papille in die interkostale streke verskil van hoog by *H. merianellum* tot laag en byna afwesig by *H. vandermerwei* en heeltemal afwesig by *H. priori*.

H. priori, met perigoniumsegmente byna ewe groot, is moontlik die primitiefste spesie van die seksie. H. vandermerwei het versmalde segmente met die anterieure segmente heelwat kleiner, en H. merianellum en H. guthriei het verbrede segmente.

1. **Homoglossum priorii** (N.E.Br.) N.E.Br. in Trans. R. Soc. S. Afr. **20:** 279 (1932).

Antholyza priori N. E. Brown 1929 p. 244, basionym—holotypus *Prior s.n.* in K. *Homoglossum revolutum* sensu Baker 1877 p. 161 pro parte, excl. syn.

Antholyza revoluta sensu Baker 1896 p. 169 pro parte, excl. syn. et var.; non Burman f. (1768), sec. N. E. Brown.

Gladiolus watsonius sensu Bolus & Wolley-Dod 1903 p. 336; sensu Marloth 1915 p. 153; sensu Smith 1926 t. 240; non Thunb. (1784).

Antholyza watsonia sensu L. Bolus 1920 p. 11 excl. syn. Thunb.

Homoglossum salteri (ined.?) is 'n tuinbouvariëteit van die spesie.

Icones: Marloth 1915 Pl.46 fig. B. sub *G. watsonius;* Flower. Pl. S. Afr. **6** t.240 (1926) sub *G. watsonius;* Kidd 1950 Pl. 28 fig. 1; Dept. Natuurbewaring t.113 sub *H. watsonium;* Mason 1972 t.26.2; Delpierre & Du Plessis 1973 fig. 24; die huidige werk fig. 11A-C.

Holotipe: Prior s.n. Julie '46 in K.

Plante 30-80 cm hoog. Knol 1,5-2 cm in deursnee, die tunicae dun, membraneus, in die onderste helfte later gesplits in filiforme gebuigde fibrille, in die boonste helfte ongesplits met 'n opgehewe arenetwerk. Stingel 30-80 cm lank. Laagteblare 2-3, tot 17 cm lank, naak. Loofblare 4 of soms 3, naak, die onderste twee die langste, tot 60 cm lank, nie tot die aar reikend, met die geribde blaarskedes baie lank, die lamina lineêr, tot 22 cm lank, 1-2,5 mm breed, geleidelik smaller na die top, met 2-3 sterk are aan elke kant en minder sterk rande; die hoogste blaar 3-7 cm lank, konduplikaat. Aar onvertak, met 2-3, of soms 1-6 eensydige blomme, die rachis dikwels golwend of soms horisontaal gebuig. Bractea lank-ellipties, rooigroen of geelgroen, 2,5-4,5 cm lank, skerp of akuminaat. Bracteola korter of soms byna so lank soos die bractea. Blomme 5.5-9 cm lank, effens gebuig en knikkend, helderrooi of soms rooi-pienk of appelkooskleurig, die keel van veral die drie anterieure segmente liggeel en soms rooi gespikkeld. Perigoniumbuis met die smal basale gedeelte 2 cm lank, die boonste silindriese deel 2-3 cm lank, ca. 5 mm in deursnee, gebuig, sonder 'n duidelike nektarsakkie; segmente byna ewe lank, smal-omgekeerd-eiervormig, smal-

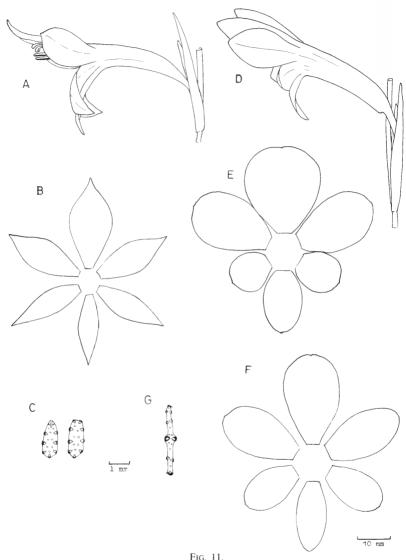


Fig. 11.

A-C, Homoglossum priorii: A, blom; B, perigoniumsegmente; C, dwarssneë deur loofblaar, links laer as regs. D-G, Homoglossum guthriei: D, blom; E, F, perigoniumsegmente van twee blomme om variasie te toon; G, dwarssnee deur blaar.

eiervormig of soms eiervormig, akuminaat of soms skerp, soms met 'n donker spikkel weerskante aan die basis, die posterieure segment omgekeerd-eiervormig, breër as die ander, reguit, 23–35 mm × 12–18 mm; top-laterale segmente spreidend, 20–32 mm × 8–12 mm; die drie anterieure segmente horisontaalspreidend tot effens teruggebuig, 20–30 mm × 6–10 mm of soms breër. Helmdrade 2–4 cm lank; helmknoppe 6–10 mm lank, donkerpers, klein-apikulaat of soms klein-ingekeep aan die toppe, reikend tot die helfte van die topblomdeksegment of effens hoër. Styl 5–6,5 cm lank, die styltakke 3–4 mm lank, rooi of pienk; stempels ca. 1 mm lank, 2 mm breed, rooi of pienk. Doosvrugte 1,5 cm of langer, wydoopsplitsend.

KAAPLAND—3317 (Saldanha): Donkergat, Langebaan (-DB), *Hall 3198* (NBG, STE).

—3318 (Kaapstad): Konstabel, Vlaeberg, W. kant van Saldanha-meer (-AA), Schelpe 5292 (BOL, SAM); Langebaan, Chaplin s.n. (NBG); Naby Mamre (-CB), Leipoldt BOL 30900, Salter BOL 21063; Top van Blouberg (-CD), Salter 5480 (BOL); Van Breda-plaas, Axelson 20 (NBG); Vlakte en bergplato by Kaapstad, Drège vindplek 86 (G); Laer dele van Tafelberg en Duiwelsberg, Burchell 8414, 8506 (K); Tafelberg bo Kirstenbosch, Esterhuysen 17284 (BOL, NBG); In rupestribus Montis Leonis, MacOwan 289 (BOL, K); Leeukop, MacOwan 2302, HNAA 289 (SAM); Oranjekloof, Gamble 22296 (K); Duiwelsberg, Krauss 1417 (G); Muldersvlei (-DD), Loubser 870 (NBG); Bottelarykop, Van Rensburg 53 (STE).

-3319 (Worcester): Waaihoek (-CB), Stokoe 8939 (BOL).

—3418 (Simonstad): Houtbaai (-AB), Alexander s.n. (K); Karbonkelberg, Chater STE 30094; Heuwel bo Kommetjie, Davis SAM 59742; Constantiaberg, Bond 1006 (NBG); Muizenberg, MacOwan 2302, HNAA 289 (SAM); Kalkbaai, Thode A165 (PRE); Imhofsgift, Barker 4576 (BOL, NBG); Simonstad, Pole-Evans 2737 (fig. in Flower. Pl. S. Afr.), Marloth 93 (PRE); Vasco da Gama-Radarstasie, Taylor 6360 (PRE, STE); Vishoek-berghange, Kensit ann. 1914 (G); Slangkopberge, Compton 13240 (NBG); Scarborough, Middlemost 1938 (NBG); Brightwater koppies (-AD), Compton 14567 (NBG); Brightwater, Kaappunt-reservaat, Leighton 421 (BOL); Steenberg-plato (-AB), Bolus 14542, 30902; Steenberg-rots, Dod 1135, 2635 (BOL, K); Palmietrivier-mond (-BD), Stokoe 8471 (BOL); Bettysbaai, Malan 11 (STE).

—3419 (Caledon): Kleinmond (-AC), *Loubser 434* (NBG); Hermanus op rotswande langs see (-AC-AD), *Galpin 12778* (PRE), *Galpin s.n.* (BOL); Elim (-DB), *Schlechter 7613* (BOL, G).

Sonder vindplek: Prior Jul. '46 (K); Elliott s.n. (G).

Volksnaam: rooi-afrikaner, rooipypie.

Blomtyd April tot Junie.

H. Bolus en Wolley-Dod (1903) het die twee spesies wat Baker (1896) onder Antholyza revoluta Burm. geplaas het, geskei as Gladiolus watsonius Thunb. (die

onderhawige spesie) en Antholyza revoluta Burm. N.E. Brown het, na 'n ondersoek van die Thunberg- en Burman-eksemplare, gevind dat Bolus en Dod se G. watsonius nie dieselfde spesie is as Thunberg s'n nie en dus nie hierdie epiteton kan dra nie. Hy moes dit daarom 'n nuwe naam, H. priorii, gee. (Sien verder onder H. watsonium)

Die blom van H. priorii lyk baie na dié van H. watsonium, met die blomdeksegmente byna ewe lank; dit mag die rede wees waarom Baker die twee spesies bymekaar geplaas het. H. priorii verskil veral in sy knoltunicae wat in besonder fyn fibrille splits, en in sy dikwels vier loofblare waarvan selfs die langste 'n kort lamina het wat nie bo die bloeiwyse uitsteek nie. Hierdie loofblaar is platter en het nie die sterk opgehewe rib in die senter en die sterk verdikte rande van H. watsonium nie, maar het twee of drie smaller are weerskante en minder sterk rande. Op die sklerenchiem van die are is groter koepelvormige epidermisselle wat dikwels in vertikale rye geleë is en die interkostale epidermisselle is sonder papillae. Die blomme verskil van die van H. watsonium ten opsigte van hul meestal meer akuminate segmente en die afwesigheid van 'n duidelike sakkie aan die blomdekbuis.

H. priorii kom hoofsaaklik in die kusdistrikte voor vanaf Saldanha tot Bredasdorp en staan dikwels in rotsskeure, somtyds taamlik naby die seekus. Die hoof verspreidingsarea is die Kaapse Skiereiland. Slegs enkele vindplekke is meer binnelands. By Mamre langs kom groter plante voor met drie laagteblare en tot ses of meer blomme (Salter BOL 21063 en Leipoldt BOL 30900) wat, volgens 'n private mededeling van prof. T. T. Barnard, onder tuinboukundiges bekend staan as H. salteri-'n ongepubliseerde naam.

Plante wat volgens Marloth skynbaar basters is tussen Gladiolus ?maculatus en G. watsonius sensu Marloth (d.i. H. priorii), is gekry op die Kaapse Skiereiland (Marloth 5689 en 5690 in BOL).

2. H. merianellum (Thunb.) Baker in J. Linn. Soc. 16: 161 (1877).

Holotipe: Thunberg 1047 in Hb. Thunberg, UPS.

Plante 30-70 cm hoog. Knol 15-25 mm in deursnee, met die tunicae in die onderste helfte gesplits in parallelle terete akuminate fibrille 0,3-0,5 mm breed, en in die boonste helfte dikwels ongesplits met opgehewe, nagenoeg parallelle are. Stingel 30-70 cm lank. Laagteblare 2, 3-10 cm lank, die tweede dikwels digbehaard na die top. Loofblare 3, korter as die stingel, lineêr, behaard met sagte syagtige hare tot 2 mm lank, die basale blaar met die blaarskede tot 20 cm lank en die lamina 7-22 cm lank, 2-5 mm breed, lineêr, met 4 sterk are en sterk rande en minder hare na die top; die tweede blaar met 'n 6-7 cm lange lamina wat unifasiaal is na die top; die derde blaar 2-7 cm lank, byna naak, soms afwesig (Goldblatt 386). Aar onvertak, met 2-6 of soms meer blomme, eensydig of in twee rye met 'n hoek van tot 60° tussenin, die rachis dikwels effens golwend. Bractea lank-eiervormig, donkerrooi tot groen, skerp, 15–25 mm lank, korter as, of so lank soos die smal basale deel van die perigoniumbuis. Bracteola omtrent so lank soos die skutblaar of effens korter, die membraneuse rand soms geoor. *Blomme* 5–7,5 cm lank, knievormig gebuig waar die perigoniumbuis verbreed, die soom bakkievormig, geel, oranjegeel of rooi. *Perigoniumbuis* met die smal basale gedeelte 10–22 mm lank, met 'n klein nektarsakkie waar dit verbreed, en die boonste silindriese deel 18–25 mm lank, 6–8 mm in deursnee, effens gebuig, byna horisontaal gestel; *segmente* byna rond tot breed-omgekeerd-eiervormig, apikulaat, die rande oorvleuelend, die posterieure segment 18–25 mm × 10–18 mm, die ander vyf segmente effens kleiner. *Helmdrade* 20–35 mm lank; *helmknoppe* 6–8 mm lank. *Styl* 4,5–6 cm lank, die takke 2–4 mm lank; *stempels* 1–2 mm lank, tot 2 mm breed, soms tot naby die top van die posterieure perigoniumsegment geleë.

Hierdie spesie kom, behalwe vir een twyfelagtige vindplek, slegs op die suidelike deel van die Kaapse Skiereiland voor, en is net eenmaal noord van Constantianek gevind. Volgens H.M.L. Bolus *e.a.* (1936) wyk die "vlamme" steeds meer na die suidelike Skiereiland, omdat dit in die winter blom en die gevleuelde saad deur die heersende noorde en noord-weste winde steeds suidwaarts gewaai word.

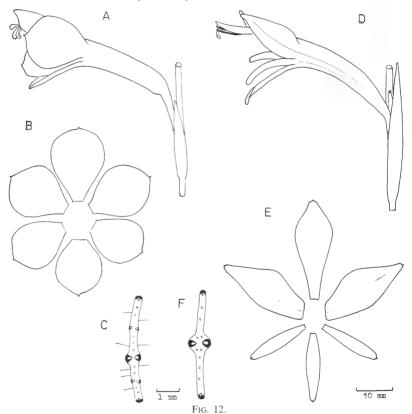
Die spesie word gekenmerk deur harige lineêre blare en geel tot oranjerooi blomme met byna ronde tot breed-omgekeerd-eiervormige segmente, die rande oorvleuelend. Daar is twee blomperiodes: plante met rooi tot oranje blomme van April tot vroeë Augustus, en plante met geel blomme van Augustus tot Oktober. Geen ander morfologiese kenmerke onderskei die twee groepe nie, en daarom word Lewis se sienswyse (1948) gevolg om hulle as variëteite van een spesie te beskou.

Milne-Redhead (1938) het die naamgewing van H. merianellum nagespeur. Dit kan soos volg opgesom word: in 1774 het Linnaeus (Murray) 'n Kaaapse plant wat as no. 60.7 in die LINN-herbarium bewaar word en wat die onderhawige Homoglossum-spesie is, breedvoerig beskryf onder die naam Antholyza merianella. Hy siteer daarby Miller (1760) se illustrasie t. 297 f.2 en beskrywende naam, van 'n plant wat egter reeds in 1768 beskryf en benaam is as Watsonia humilis. Linnaeus se naam A. merianella is dus nomenklatories oorbodig en moet verwerp word en sy plant was dus nog sonder 'n geldige naam. In 1784 beskryf Thunberg 'n plant wat hy aan die Kaap versamel het en wat identies is met LINN no. 60.7, behalwe vir die blomkleur, as Gladiolus merianellus. Hy gee sy eie beskrywing en siteer geen sinonieme daarby nie, nòg die van Linnaeus soos Milne-Redhead beweer het, nog van Miller. Thunberg was dus die eerste om die naam Gladiolus merianellus vir die onderhawige spesie geldig in te stel, en vir prioriteit dateer die naam van 1784 en nie van 1774 nie. (Later, in 1794 en daarna, siteer Thunberg by G. merianellus wel Linnaeus se plantnaam as sinoniem; maar dit maak nie sy naam van 1784 ongeldig nie.)

Milne-Redhead (1938) beskou die epiteton *merianella*, 'n verkleinwoord is van *Meriana*, as 'n selfstandige naamwoord in apposisie en nie verbuigbaar nie. Saam met werkers soos N. E. Brown (1932), Lewis (1948, 1950) en prof. T. T. Barnard

(private mededeling), beskou ek dit as 'n byvoeglike naamwoord en verbuig dit dus.

Linnaeus (Murray 1774, 1784) beskryf die plant LINN no. 60.7 se blomme as geel en daarom word dit nou onder die var. *aureum* gesiteer. Thunberg beskryf sy plant as "flavo-incarnati", d.w.s. geel-vleeskleurig, en dit sou dus onseker wees aan watter van die twee variëteite sy plant behoort, was dit nie dat daar, volgens Juel (1918), 'n aantekening van Klatt op Thunberg se eksemplaar in sy herbarium is wat vermeld: "Fl. rose!" en dat Thunberg in sy *Flora Capensis* van 1807 aanteken dat die plant in Februarie, Maart en April blom nie. Hierdie twee kenmerke is dié van die tipiese oranjerooi variëteite.



A-C, Homoglossum merianellum: A, blom; B, perigonium; C, dwarssnee deur loofblaar. D, E, F, Homoglossum vandermerwei: D, blom; E, perigoniumsegmente; F, dwarssnee deur blaar.

SLEUTEL VIR DIE TWEE VARIËTEITE

a. var. merianellum

Homoglossum merianellum (Thunb.) Baker 1877 p. 161 excl. syn. L.; N. E. Brown 1932 p. 279; Bolus, Barclay & Steer 1936 p. 177; Milne-Redhead 1938 t. 9510; Lewis 1950 p. 263 excl. syn. L.; Lewis, Obermeyer & Barnard 1972 p. 301; Du Plessis & Delpierre 1973 p. 49; Delpierre & Du Plessis 1973 p. 34.

Gladiolus merianellus Thunberg 1784 p. 168, basionym, & 1794 p. 7 excl. syn., & 1807 p. 172, & 1823 p. 41 excl. syn. L.—holotypus Thunberg 1047 in Hb. Thunb., UPS; Willdenow 1797 p. 214 excl. syn. L. & Mill.; Vahl 1805 p. 95 excl. id. syn.; Poiret 1812 p. 788 excl. id. syn.; Roemer & Schultes 1817 p. 422 excl. id. syn.; Ker 1827 p. 133 excl. syn. L.; Klatt 1882 p. 341; Pax 1888 p. 156; Baker 1892 p. 227 excl. syn. L.; Klatt 1895 p. 220 excl. syn. L. et Jacq.; N. E. Brown 1928 p. 26 excl. syn.

Antholyza merianella (Thunb.) Baker 1896 p. 169, non L.; H. Bolus & Wolley-Dod 1903 p. 337; Marloth 1915 p. 160; L. Bolus 1924 p. 8; N. E. Brown 1928 p. 26; Diels 1930 p. 495; non L. (Murray) 1774 & 1784.

Gladiolus hirsutus Jacq. var. tenuiflorus Ker 1802 sub. t. 574. G. hirsutus (β) var. merianellus Ker 1804 sub. t. 727; Sprengel 1825 p. 152.

Watsonia humilis Persoon 1805 p. 42 excl. syn. Mill. et L.

W. pilosa Klatt 1885 p. 200—holotypus Macowan 2510B.

[Gladiolus tubulosus in LINN. et G: auct. non Burm. 1768, nec Jacq. 1790.]

Icones: Marloth 1915 t. 48D; L. Bolus 1924 p. 5; Hamer 1926 p. 89 fig. 5; Levyns 1929 p. 84; Bolus, Barclay & Steer 1936 p. 178; Curtis's bot. Mag. 160 t. 9510 (1938); Kidd 1950 t. 35 fig. 1; Dept. Natuurbewaring 1958 t. 111; Du Plessis & Delpierre 1973 p. 49; Delpierre & Du Plessis fig. 28, 29; die huidige werk Fig. 12A-C.

Hierdie variëteit se blomme varieer van rooi tot oranjerooi (RHS 25A binne, 31A, 32B buite) moontlik deels afhangende van die ligintensiteit. Plante met oranjerooi blomme het rooi spikkels in die keel en is rooierig getint buite.

KAAPLAND—3318 (Kaapstad): Tafelberg (-CD), Molteno Fl. S.A. 22125 (K).
—3418 (Simonstad): In clivis montis Muizenberg (-AB), Bolus 4869 (BOL, K); In rupestribus montium pone Simonstown, MacOwan & Bolus HNAA 290 (BOL, STE, PRE, G); Naby Simonstad, Pappe SAM 21524, MacOwan HAA 1551, HNAA 290 (SAM, K), Zeyher 236 (PRE, SAM), Garside 1047 (K); Berge naby Simonstad, Prior PRE 32585, Dümmer 1571 (SAM); Red Hill, s. coll. (K); Hange tussen Steenberg-plato en Noordhoek-berge, Hamer BOL 25341; Silvermine-plato, Goldblatt 386 (BOL); Naby Klaasjagers, Linley SAM 59741; Klavervlei, Pillans PRE 32586, Salter s.n. (K); Millers Point, Thode 5420 (STE); Plato

bo Smitswinkelbaai (-AD), *Phillips s.n.* ann. 1912 (G); Patrysvlei, *Dod 1243* (BOL, K); Kaappunt, *Minicki* NBG 269/41; Sir Lowryspas (-BB), *Galpin 3520* (BOL, PRE); In summitate montium inter Noordhoek & Bayfals (sec. Thunberg, 1807), *Thunberg 1047* (UPS).

C.B.S. sonder vindplek: HB Burman, sub *Gladiolus tubulosus* Thunb. (Thunb. scrpsit, G).

Blomperiode April tot vroeë Augustus, en volgens Thunberg vanaf Februarie. Populêre naam: vlamme, ''flames''.

b. var. **aureum** Lewis in Jl S. Afr. Bot. **14:** 34 (1948) & 1950 p. 263. *Antholyza merianella* L. (Murray) 1774 p. 77 & 1784 p. 87, uterque quoad descr., nom. superfl.; sensu Houttuyn 1780 p. 81 excl. ic. Miller; sensu Persoon 1797 p. 89 excl. ic. Miller.

Icones: Du Plessis & Delpierre 1973 p. 49; Delpierre & Du Plessis 1973 Fig. 30.

Holotipe: Linley SAM 58293 in SAM. Isotipe in BOL.

Hierdie variëteit is in alle opsigte soos die tipiese variëteit, behalwe vir sy oranjegeel of goudgeel kleur (RHS 32C) en sy latere blomperiode, Augustus tot Oktober.

KAAPLAND—3418 (Simonstad): Tussen Scarborough en Klaasjagers (-AB), Linley SAM 58293 (BOL, SAM); Naby Klaasjagers, Barker 5906 (NBG); Vlakte oos van Klaasjagers, Goldblatt 459 (BOL); Kaappunt-Natuurreservaat, nat sandvlakte noord van Teeberg, de Vos 2302 (STE); Kaappunt-Natuurreservaat, nat sandvlakte, Taylor 8617 (STE); In arenosis Muizenberg, Marloth 115 (PRE); Simonstad, Dodd 1694 (K); Red Hill, Taylor s.n. (NBG); Suidelike punt van die Kaapse Skiereiland (-AD), Darroll BOL 17283. Rogers 1/80 van Simonsbaai (K) is waarskynlik hierdie variëteit.

Linnaeus (Murray, 1774, 1784), Houttuyn (1780) en Persoon (1797) beskryf die blomme van die plant as geel en daarom word hul beskrywings as dié van var. *aureum* beskou.

3. **Homoglossum guthriei** (L. Bol.) L. Bolus in S. Afr. Gard. & Country Life **23:** 47 (1933); E. P. Phillips 1941 p. 44.

Antholyza guthriei L. Bolus 1920 p. 12, basionym—syntypi Guthrie 3827 & BOL 14954 in BOL.

Petamenes guthriei (L. Bol.) N. E. Brown 1932 p. 276.

Icones: Goldblatt 1971 p. 407 Fig. 24f; 'n ongepubliseerde gekleurde tekening deur W. F. Barker in BOL; die huidige werk Fig. 11D-G.

Lektotipe: Guthrie 3827 in BOL.

Plante 35–55 cm hoog. Knol 12–15 mm in deursnee, tunicae membraneus, later in die onderste helfte van die knol gesplits in fyn parallelle, filiforme, gebuigde fibrille, na bo ongesplits en met 'n opgehewe arenetwerk. Stingel 35–55 cm lank.

Laagteblare 2, 4-8 cm lank, stomp. Loofblare 4 tot soms 6, lineêr, tot 30 cm lank, maar steeds korter as die stingel, die onderstes met die fyn geribde skede tot 12 cm lank, en die unifasiale lamina tot 20 cm lank, 3-6 mm breed, met 1-3 sterk are en soms sterk rande en met haarstompies op die kostale stroke, die boonste blare 5-10 cm lank en unifasiaal vir slegs die top 1-4 cm. Aar met 2-8 of meer blomme of soms net een, eensydig. Bractea smal-eiervormig tot smal-ellipties, rooigroen, 4-5.5 cm lank, skerp tot stomp, effens hoër reikend as die top van die smal basale gedeelte van die blomdekbuis. Bracteola effens groener en korter as die bractea. Blomme 7-9,5 cm lank, effens gebuig, half-stygend, die posterieure segmente rooi of oranjerooi met donkerrooi spikkels en strepe, die anterieure geel, oranjegeel of rooi met 'n geel keel. Perigoniumbuis met die smal basale gedeelte 18-20 mm lank, met 'n baie klein sakkie waar dit skielik verbreed, die boonste silindriese gedeelte 20-35 mm lank, 6-7 mm in deursnee, gebuig; segmente omgekeerd-eiervormig of ellipties tot nagenoeg rond, stomp of soms kleiningekeep, die posterieure segment reguit, 15-25 mm × 10-23 mm, effens konkaaf, omgekeerd-breed-eiervormig; top laterale 15–25 mm × 8–15 mm, ellipties, effens spreidend, met donkerrooi strepe; anterieur-laterale 8-12 mm × 5-12 mm, nagenoeg rond tot ellipties, spreidend en effens teruggebuig, anterieurmediaan 12-18 mm × 6-10 mm, ellipties, spreidend of effens teruggebuig. Helmdrade 3,5-4,5 cm lank; helmknoppe 5-8 mm lank, stomp, geel. Styl 6,5-7 cm lank, styltakke 4-5 mm lank; stempels 2 mm lank, 3-4 mm breed, diepgekeep, later tot die top van die top-mediane segment reikend.

KAAPLAND—3419 (Caledon): Naby Stanford (-AD), *Lindley* NBG 535/49; Tussen Stanford en Gansbaai (-AD-CB): *Esterhuysen* BOL 30891; Witvoetskloof (-CB), *Yeats s.n.* (STE), *Woods 1* (NBG); Tussen Gansbaai en Dangerpoint, *Stokoe* SAM 55628; Noordekant van Paardeberg, Stanford-Caledonpad (-AD), *Chater s.n.* (NBG); Naby Elim (-DA-DB), *Bolus* BOL 30890, *Guthrie* 3827 (BOL); Strandkloof kalkrif (-CB), *Oliver s.n.* 3.9.66 (STE); Pearly Beach (-DA), *Lawder* NBG 519/73.

Hierdie spesie het 'n beperkte verspreiding in die Caledon en Bredasdorpdistrikte. Dit blom dikwels op veld wat die vorige somer afgebrand was.

Die blomme varieer in grootte en in die breedte van die segmente; by voorbeeld, by die sintipe BOL 14954 is sommige blomme klein, met al die segmente ellipties of smal-ellipties; terwyl die anterieur-laterale segment rond is by ander versamelings (bv. Leighton BOL 21244), en die posterieuse segment byna rond.

Volgens L. Bolus is *H. guthriei* naverwant aan *Antholyza quadrangularis* Burm. (waarmee sy *H. abbreviatum* bedoel het), waarvan dit verskil in die besit van vier korter blare met rande nie so erg verdik nie. Weens hierdie sienswyse plaas N.E. Brown die spesie in die genus *Petamenes*. Hy het egter erken dat hy nie 'n voorbeeld van die spesie gesien het nie. Volgens 'n ongepubliseerde aantekening van G. J. Lewis in BOL is dit naverwant aan *H. fourcadei* en sy kon nie insien

waarom Brown dit in 'n aparte genus, *Petamenes*, plaas nie. Die blaaranatomie verskil egter heelwat van die 4-vleuelige blaar van *H. fourcadei*. Heelwaarskynlik staan dit naaste aan *H. merianellum* wat ook lineêre blare het met interkostale epidermale papille en breë perigoniumsegmente wat dikwels stomp is.

4. Homoglossum vandermerwei (L. Bol.) L. Bolus in S. Afr. Gard. & Country Life 23: 47 (1933).

Antholyza vandermerwei L. Bolus 1931 p. 14, basionym—holotypus Van der Merwe BOL 19084.

Icones: Goldblatt 1971 p. 407 Fig. 24g; Delpierre & Du Plessis 1973 Fig. 71; ongepubliseerde tekeninge in BOL en NBG; die huidige werk Fig. 12D-F.

Holotipe: Van der Merwe BOL 19084 in BOL.

Plante 35-60 cm hoog. Knol 8-12 mm in deursnee, met ligbruin membraneuse tunicae gesplits in filiforme gebuigde parallelle fibrille, na bo ongesplits met 'n opgehewe arenetwerk. Stingel sterk, 35-60 cm lank, tot 5 mm in deursnee, soms met een of twee takke uit die boonste skutblaaragtige blare. Laagteblare 2, naak, tot 12 cm lank, rooibruin gespikkeld. Loofblare 5-7, naak, tot 40 cm lank, 2-5 mm breed, korter as die stingel of soms langer, die onderstes met die lang geribde blaarskede rooibruin gespikkeld, die lamina lineêr, 15-30 cm lank, met smal, opgehewe "middelaar" en effens versterkte rande; die hoër blare 3-15 cm lank, bifasiaal of unifasiaal na die punte. Aar onvertak of met een of twee takke aan die basis, met 4-6 blomme per tak, die rachis soms effens golwend. Bractea byna lineêr, groen of rooigroen, 4-6 cm lank, half-stomp. Bracteola smal-eiervormig, korter as die bractea. Blomme 6,5-9,5 cm lank, krom, vermiljoen of oranjepienk (bv. RHS 41B), die anterieure segmente groengeel of geel met 'n groenerige mediane strook, die toppe pienk. Perigoniumbuis 4-6,5 cm lank, die smal basale gedeelte 15-20 mm lank, sonder 'n nektarsakkie, geleidelik verbreed onder die middel, die silindriese boonste gedeelte effens gebuig, 25-45 mm lank, ca. 5 mm in deursnee; segmente stomp, apikulaat of soms ingekeep, die drie posterieure segmente reguit, smal-eiervormig of smal-omgekeerd-eiervormig, 22-30 mm × 6-12 mm, met die twee laterale segmente dikwels breër as die mediane en skeef, met hul helftes verskillend in breedte; die drie anterieure segmente baie smaller, nagenoeg lineêr, spreidend of teruggebuig, soms effens gedraai, 15-20 mm × 2-4 mm, die mediane segment effens groter as die twee laterale. Helmdrade 3-5 cm lank; helmknoppe 7-9 mm lank, soms klein apikulaat, geel met rooi lengtestrepe, soms tot naby die top van die top-mediane segment reikend. Styl 6-7,5 cm lank, die styltakke 5 mm lank, smal; stempels smal, pienk, 3 mm lank, 1 mm breed, die wit papilleuse rande 3 mm lank, reikend tot naby die top van die mediane topsegment.

KAAPLAND—3320 (Montagu): Bonnievale (-CC), Van der Merwe 17 (BOL). —3419 (Caledon): Tussen Botrivier en Houhoek (-AA), Guthrie BOL 16908; 5 ml van Napier na Caledon (-BD), Barnard NBG 2040 β2 (BOL), Malan 12 (STE).

—3420 (Bredasdorp): Kathoek, kus-renosterveld (-AD), *Acocks* 22599 (PRE); Hasiesdrift tussen Swellendam en Bredasdorp (-AC), *Lewis* 6082 (NBG); Naby Swellendam (-AB), *Van der Merwe* BOL 19084, ex hort. Smith BOL 19967 (BOL, K); Tussen Vermaaklikheid en Fort Beaufort (-BD), Lewis 5998, 6012 (NBG); Duiwenhoksrivier, 5 ml NW van Vermaaklikheid (-BB/BD), *Acocks* 21577 (NBG), *Lewis* 5998 (STE).

Blomtyd Augustus-September.

Hierdie spesie, wat hoofsaaklik in die suidelike kusdistrikte vanaf Caledon tot Riversdale voorkom, word gekenmerk deur sy knol met fyn, filiforme fibrille, 'n dikwels vertakte stingel (die enigste *Homoglossum*-spesie waar vertakking voorkom), meer as drie kort, lineêre blare met smal sklerenchiemstroke op die rande en in die middel, en blomme met die drie anterieure segmente baie smaller en effens korter as die posterieure segmente, en met skraal, verlengde stempels.

Gekweekte plante (BOL 19967 in BOL en K) is groter as wat in die beskrywing hierbo aangegee is, bv. tot 85 cm hoog, met blare tot 60 cm lank en 7 mm breed.

Die spesie verskil van die tipiese homoglossums dáárin dat die perigoniumbuis wat sonder nektarsakkie is, nie baie skielik verbreed by sy middel nie. Daar die boonste deel van die buis silindries is soos tipies vir *Homoglossum* en nie tregtervormig soos by *Gladiolus* nie, word dit tog by *Homoglossum* geplaas.

2. SEKSIE HOMOGLOSSUM

Die twee spesies van hierdie seksie word gekenmerk deur verhoute knoltunicae wat vanaf die knolbasis gesplits is in harde gebuigde elsvormige slippe, meer as 1 mm op hul breedste. In die boonste helfte is die tunicae ongesplits met 'n gladde oppervlak. Die lamina van die basale loofblaar het vier sterk ribbe. Die dorsale en ventrale ribbe is eenders, met 'n breë subepidermale sklerenchiemlaag, een groot vaatbundel en verskeie kleineres weerskante van die grote. Die ribbe van die hooflaterale vaatbundels (die ''middelaar'') verskil: by *H. muirii* is hulle identies met die dorsale en ventrale ribbe; by *H. watsonium* daarenteen is hulle smaller, met slegs twee klein vaatbundels weerskante van die groot bundel. Die blaar van *H. muirii* vertoon dus byna tereet, maar met vier smal diagonaal geplaasde lengtegroewe, terwyl dié van *H. watsonium* platterig is met breë verdikte rande en effens smaller verdikte ''middelaar''-ribbe (Fig. 2E, G).

Die perigoniumsegmente van *H. watsonium* is byna ewe lank, terwyl dié van *H. muirii* in lengte verskil. Om hierdie rede word die e.g. meer primitief as die lg. beskou.

Homoglossum watsonium (Thunb.) N. E. Brown in Trans. R. Soc. S. Afr. 20: 277, 278 (1932); Lewis 1950 p. 263; Lewis, Obermeyer & Barnard 1972 p. 301 & 303; Du Plessis & Delpierre 1973 p. 58; Delpierre & Du Plessis 1973 p. 40.

Gladiolus watsonius Thunberg 1784 p. 167, & 1794 p. 8, & 1807 p. 173, & 1823 p. 41, basionym—holotypus *Thunberg 1092* in Hb. Thunb., UPS; Jacquin 1789 p. 257 & 1792 t. 233; Willdenow 1797 p. 214; Ker 1799 t. 450, & 1805 p.

230, & 1827 p. 130 excl. syn. Burm.; Vahl 1805 p. 123 excl. syn. Burm.; Aiton 1810 p. 96; Poiret 1812 p. 787 excl. syn. Burm.; Redouté 1813 t. 369; Roemer & Schultes 1817 p. 421 excl. syn. Burm.; Sprengel 1825 p. 152; Loddiges 1833 t. 1949; Klatt 1863 p. 716, & 1882 p. 341, & 1895 p. 277 excl. syn. Burm.; Baker 1892 p. 227 excl. id. syn; N. E. Brown 1929 p. 243; non sensu Bolus & Wolley-Dod 1903, nec Marloth 1915, nec Smith 1926. *G. watsonius* Thunb. var. *b* Ker 1802 sub t. 569. *G. watsonius* Thunb. var. *gawleri* (Klatt) Baker 1892 p. 227.

Gladiolus angustus sensu Burman f. 1768 p. 2 pro parte—typus Hb. Burman in G; non Linn. 1753.

G. recurvus sensu Houttuyn 1780 p. 49 & t. 79 Fig. 1—holotypus Hb. Burm. in G; non Linn. 1767, nec Miller 1760.

G. praecox Andrews 1797 t. 38 var. flore rubro Andr.—iconotypus Bot. Rep. t. 38.

Watsonia praecox (Andr.) Persoon 1805 p. 42.

Homoglossum praecox (Andr.) Salisbury 1812 p. 325.

Watsonia revoluta Persoon 1805 p. 42.

Homoglossum revolutum (Pers.) Baker 1877 p. 161 pro parte, excl. syn. Burm. H. revolutum Bak. var. gawleri (Klatt) Baker 1877 p. 161—iconotypus Curtis's bot. Mag. t. 569.

Antholyza revoluta (Pers.) Baker 1896 p. 169 pro parte, non Burm. 1768 (nom. dub.); Bolus & Wolley-Dod 1903 p. 336; Marloth 1915 p. 161; Diels 1930 p. 495; semper auct. non Burm. 1768. A. revoluta Bak. var. gawleri (Klatt) Baker 1896 p. 169.

Gladiolus gawleri Klatt 1882 p. 341 & 1895 p. 217 excl. syn. Watsonia pilosa—iconotypus Curtis's bot. Mag. t. 569.

Antholyza gawleri (Klatt) L. Bolus 1920 p. 11.

Homoglossum gawleri (Klatt) N. E. Brown 1932 p. 278; L. Bolus 1933 p. 46.
Antholyza watsoniana (Thunb.) pro watsonium Pax 1888 p. 156—holotypus Thunberg 1092 in UPS; N. E. Brown 1929 p. 244.

Homoglossum watsonianum (Pax) N. E. Brown 1932 p. 277.

Antholyza acuminata N. E. Brown 1929 p. 133—holotypus Burman s.n. sub Gladiolus recurvus in G.

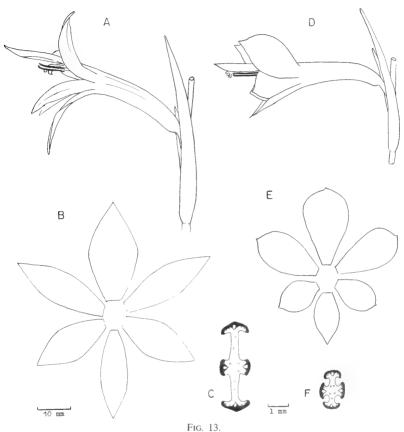
Homoglossum acuminatum (N.E.Br.) N. E. Brown 1932 p. 278.

H. flexicaule N. E. Brown 1932 p. 279-holotypus Villett s.n. in K.

Icones: Houttuyn 1780 t. 79 Fig. 1; Andrews 1797 t. 38; Curtis's bot. Mag. 13 t. 450 & 16 t. 569; Jacquin Ic. t. 233; Redouté 1813 t. 369; Loddiges 1833 t. 1949; Marloth 1915 t. 50B; Stoneman 1915 p. 28, 167; Hamer 1926 p. 91 Fig. 7; Nature Notes 4 no. 33; Rice & Compton 1950 t. 211; Kidd 1950 Pl. 47 Fig. 1; Dept. Natuurbewaring t. 112 sub *H. priorii*; Du Plessis & Delpierre 1973 no. 24. Delpierre & Du Plessis 1973 Fig. 45; die huidige werk Fig. 13A-C.

Holotipe: Thunberg 1092 sub G. watsonius in Hb. Thunberg, UPS.

Plante 40 cm tot 1 m hoog of hoër. Knol breed by die basis, 15-25 mm in



A-C, Homoglossum watsonium: A, blom; B, perigoniumsegmente; C, dwarssnee deur blaar. D-F, Homoglossum muirii: D, blom; E, perigoniumsegmente; F, dwarssnee van blaar.

deursnee, met harde houterige tunicae wat vanaf die basis tot bo die middel in breë akuminate slippe, 1–2 mm wyd, gesplits is en na bo ongesplits en glad, dikwels met talryke klein sittende byknolletjies aan die knolbasis. *Stingel* 30–75 cm lank. *Laagteblare* 2, 2–18 cm lank, naak, skerp tot stomp. *Loofblare* 3, naak, die basale blaar langer as die bloeistingel of soms korter, met die geribde blaarskede 15–25 cm lank en die unifasiale lamina 45–100 cm lank, 1–5 mm breed, lineêr met 'n sterk, opgehewe rib in die middel, en nog sterker, breër ribbe op die rande; die tweede met 'n lang geribde blaarskede wat die stingel tot

naby die aar bedek, en 'n lamina 5-12 cm lank, met die top soos by die eerste blaar; die derde blaar 6-16 cm lank, konduplikaat. Aar onvertak, met 2-6 eensydige blomme, die rachis soms horisontaal. Bractea smal-eiervormig, groen, 4,5-6,5 cm lank, skerp tot half-stomp. Bracteola korter as die bractea. Blomme 7,5-10 cm lank, gebuig, helderrooi tot oranjerooi (RHS 33A, 34A, 43A, 44B). gelerig diep in die keel. Perigoniumbuis met die smal basale gedeelte 16-25 mm lank, met 'n klein nektarsakkie, en soms byna reghoekig gebuig waar die buis verbreed, en met die boonste silindriese deel 25-30 mm lank, 5-7 mm in deursnee, effens gebuig; segmente ellipties of smal-ellipties, byna ewe lank, ongeveer so lank soos die breë deel van die blomdekbuis, skerp of akuminaat, die posterieure segment breër as die ander, effens konkaaf, reguit, 28-33 mm × 12-16 mm, dikwels half-deurskynend na die basis; posterieur-laterale 25-35 mm × 8-11 mm, spreidend; die drie anterieure segmente effens teruggebuig, 20-35 mm × 7-10 mm, met die mediane dikwels langer en effens smaller as die laterale segmente. Helmdrade 3,5-4 cm lank; helmknoppe 7-10 mm lank, donkerpers met liggeel pollen. Styl 6-7 cm lank, die styltakke 4-6 mm lank; stempels oranjerooi, 2 mm lank, tot 4 mm breed. Doosvrugte tot 4,5 cm lank.

KAAPLAND—3318 (Kaapstad): Heuwel NW van Contreberg (-AD), Pillans 6897 (BOL); Darling, Kensit BOL 13675, Bolus 20178; Groote Post, Salter 6860 (BOL); Tussen Mamre en Malmesbury (-BC), Garside 4634 (K); Tussen Eikeboom en Riebeeck Kasteel, Drège 8448b (K); Mamre-weg (-CB), Thorne SAM 53123; Kaapstad (-CD), Rogers 28317 (SAM, K); Prior PRE 32588; De Waalweg. Salter BOL 30903: Universiteitsgronde, Compton 8930 (NBG); Ad latera montium praecipue in Leuwestaart, juxta Constantium e.a., Thunberg (UPS); In clivis asperis montis Diaboli prope Mowbray, Bolus 3729 (BOL, K); Onder Prins van Wallis-Blokhuis, Dod 1313 (BOL, K); Leeukop, Marloth 10091 (PRE, STE), Pappe SAM 21521; Ad dorsum Leonis, Ecklon ann. 1928 (G, K); Montagne de Lion Sud, Verreaux s.n. (G); Kampsbaai, Thode 8528 (STE); Koniklike Sterrewag, Observatory, Davis SAM 49625; Rondebosch, Lewis 718 (SAM); Naby Mostertskloof Mowbray, Dod 3036 (K); Durbanville-Klipheuwel-pad (-DA-DC), Van Niekerk 152 (BOL, NBG, PRÉ); Suide kante van Tygerberg (-DC), Pillans 8539 (BOL); De Grendel, Weste hange van Tygerberg, Esterhuysen 23058 (BOL); Tussen Durbanville en Paarl (-DC-DB), Lewis BOL 30888; Naby Wellington (-DB), Grant 2358 (BOL, PRE); Tygerberg-heuwels (-DC), Laubscher s.n. Aug. 1971 (STE); Plaas Verona, Durbanville, Bos 463 (K); Naby Peaslake, Durbanville, Taylor 1655 (NBG); Hasendal, Kuilsrivier, Rycroft 2293 (NBG); NW van Fisantekraal-stasie, Thompson 735 (STE); Heuweltop, Stellenbosch (-DD), Duthie 862a (STE-U); Groot Drakenstein, Duthie 862 (STE-U); Bottelary, Schmidt s.n. (STE); Noordelike rug van Papegaaisberg, Taylor 7332 (STE); Botmaskop, Strey 546 (PRE): Durbanville-Agter-Paarl-pad, De Vos 2316 (STE).

—3319 (Worcester): În collibus pone Porterville (-AA), Schlechter 10714 (BOL, PRE, K); În planitie pr. Piketberg Road (= Gouda) (-AC), Schlechter 4841 (BOL,

PRE, SAM, K); Mostertshoek, Romansrivier, De Vos 2287 (STE); Tulbagh, Winterhoek-West begraafplaas (-AA), De Vos 2322 (STE).

C.B.S. sonder nadere vindplek: Drège 8448a (G); Verreaux s.n. (G); Roxburgh s.n. (G); Schlechtendal 1926 (G); Hb Burman sub Gladiolus angustus Pluk. 187 (G); Hb. Burman sub G. recurvus (G); Zeyher 3975 (G). Villett s.n. sub H. flexicaule (K).

Blomtyd Mei-September.

Baker (1877, 1896) het twee spesies onder een naam, *Homoglossum* (of *Antholyza*) revolutus geplaas. H. Bolus en Wolley-Dod (1903) het hulle geskei as *Gladiolus watsonius* Thunb. en *A. revoluta* Burm., maar Brown (1929) het gevind dat die eersgenoemde spesie nie Thunberg se *G. watsonius* is nie. Hy het dit 'n nuwe naam, *H. priori*, gegee. Die tweede, wat H. Bolus en Wolley-Dod *A. revoluta* Burm. genoem het, het Brown gevind die ware *G. watsonius* Thunb. te wees, en het dit sy geldige epiteton teruggegee. Hy het verder gevind dat daar geen eksemplaar van *A. revoluta* Burm. in die Burman-herbarium is nie en, omdat Burman die jongere se beskrywing (1768) nie duidelik is nie, het hy hierdie spesie as onseker beskou. Hierdie naam kan gevolglik nie gebruik word soos Baker dit gedoen het nie, daar nog steeds onsekerheid bestaan oor wat Burman met *A. revoluta* bedoel het.

H. watsonium is taamlik variërend wat die lengte en breedte van sy lang basale loofblaar betref, asook die breedte en skerpte van die blomdeksegmente.

Die spesie verskil van die ander homoglossums in sy blaaranatomie: die lang basale loofblaar het sy rande en middelste aar (d.i. die hooflaterale) sterk opgehewe en verbreed deur middel van breë sklerenchiemribbe. Die sklerenchiemribbe van die hooflaterale (wat in die middel van die blaaroppervlakte lê) is effens smaller as dié van die rande (Fig. 2E). Tweedens verskil dit van die ander Homoglossum-spesies, behalwe H.muirii, in sy harde, verhoute knoltunicae wat in die onderste helfte in breë spits slippe, 1–2 mm breed, splits, terwyl die boonste gedeelte ongesplits en glad is. Derdens verskil dit van al die homoglossums, behalwe H.priori, in sy byna ewe lange blomdeksegmente. Anders as by die laasgenoemde, is hier 'n nektarversamelsakkie aan die blomdekbuis en is sy blomdeksegmente meestal effens minder akuminaat.

Anders as *H. priori*, kom *H. watsonium* nie in die suidelike deel van die Kaapse Skiereiland of na Caledon se kant voor nie; wel in die noordelike Skiereiland en meer binnelands, vanaf die Piketberg-distrik oor Malmesbury na Wellington, Tulbagh, Worcester en Stellenbosch, hoofsaaklik op Malmesbury-skalie.

Omdat *H. watsonium* in die onmiddellike omgewing van die Kaap voorkom, is dit alreeds vanaf die agtiende eeu bekend in Engeland en Europa waar dit gekweek, geïllustreer en beskryf is onder verskeie name, weens die variasies wat opgemerk is in o.a. die kromming van die rachis en die breedte en kleur van die blomdeklobbe. Twee van hierdie spesiesname het as tipes slegs tekeninge, sover nagegaan kon word.

Die tipe van *H. gawleri* is 'n gekleurde illustrasie in die Curtis's bot. Mag. tab. 569 van 'n kleinerige plant wat uit Holland verkry is, met groterige rooi blomme met die blomdekbuis en die blomdeksegmente tot by hul middel geel en rooi gestreep. Ker vermeld hier dat hy vermoed dat die plant in Holland van saad gekweek is, daar hy dit nog nooit tevore in enige herbarium gesien het nie, of by enige besending wat direk van die Kaap gekom het nie. Hy beskou dit as 'n variëteit wat min, behalwe in blomkleur, verskil van die reeds in tab. 450 geïllustreerde *G. watsonius*. Daar die tipetekening van *H. gawleri* slegs in sy geler blomdek van *H. watsonium* verskil (die knol word ongelukkig nie getoon nie), word die spesie na die sinonomie van *H. watsonium* verplaas. Die posterieure blomdeksegment by *H. watsonium* is dikwels effens deurskynend na sy basis, wat daaraan 'n gelerige voorkoms verleen.

Die tipe van *H. praecox* is Andrews se tekening (1797) wat hy beskryf as 'n *Gladiolus* met swaardvormige blare gedraai aan die punte, lineêr en kruisvormig, blomme byna klokvormig en rooi, met skerppuntige lobbe. Die blaar in die tekening lyk korrek vir *H. watsonium*, behalwe dat dit effens breër is as wat in die veld aangetref word, maar nie veel breër as by gekweekte plante nie.

Die tipe van *H. acuminatum* in die Burman-herbarium is sonder 'n knol of basale loofblaar. Die tweede loofblaar is egter tipies vir *H. watsonium* en die smal, skerp perigoniumsegmente word ook dikwels as 'n variasie by *H. watsonium* aangetref. Daar die tipe-eksemplaar geen kenmerk vertoon wat dit van hierdie spesie kan afskei nie, word *H. acuminatum* as sinoniem van dié spesie beskou.

Die tipe van *H. flexicaule* in die Kew-herbarium is 'n *H. watsonium* met 'n bloeistingel wat horisontaal gebuig is en met effens smaller blomdeksegmente—dit is variasies wat soms voorkom.

Volksname: suikerkane (v. Thunberg, 1823: Zuykerkan), uitsuiertjie, rooi-Afrikaner.

Homoglossum muirii (L. Bol.) N.E.Br. in Trans. R. Soc. S. Afr. 20: 279 (1932). Delpierre & Du Plessis 1973 p. 42.

Antholyza muirii L. Bolus 1920 p. 12—syntypi Muir 1348 & BOL 14953 in BOL.

Icones: Delpierre & Du Plessis Fig. 47; die huidige werk Fig. 13D-F. Lektotipe: Muir 1348 in BOL; isotipe in SAM.

Plante 30–60 cm hoog. Knol 15–20 mm in deursnee, met harde, houterige tunicae van onder tot bo die middel gesplits in harde akuminate slippe 1–2 mm breed, in die topgedeelte opgesplits en glad. Stingel 30–60 cm lank. Laagteblare 2, tot 10 cm lank. Loofblare 3, die basale blaar so lank soos die stingel of korter of selde langer, met die lang geribde blaarskede 12–20 cm lank, en die unifasiale lamina pseudo-tereet, 10–30 cm lank, 1–1,5 mm in deursnee, met 4 sterk, ewe breë ribbe dikwels met klein haarstompies op die rande van die ribbe, en 4 diep diagonaal-gestelde groewe; die tweede blaar grootliks bifasiaal, met slegs die top

soos die basale blaar; die derde tot 10 cm lank, konduplikaat tot oopgevou. Aar onvertak, met 2-5 blomme meestal na die een kant gedraai, regop of soms gebuig. Bractea smal-eiervormig, groen of rooigroen, 3–5 cm lank, stomp tot skerp, langer as die smal deel van die blomdekbuis. Bracteola korter en dikwels verberg onder die bractea. Blom 5-7 cm lank, gebuig, rooi (RHS 40A, 41A) tot diep-oranie, die keel geel. Perigoniumbuis met die smal basale gedeelte 10-15 mm lank, krom, met 'n klein nektarsakkie waar dit verbreed, die boonste silindriese gedeelte 25-30 mm lank, 4-5 mm in deursnee, nagenoeg horisontaal gestel; segmente ellipties tot eiervormig of omgekeerd-eiervormig, apikulaat of skerp, slegs een-kwart tot een-derde die lengte van die blomdekbuis, en ook meestal korter as die silindriese boonste deel van die buis, die posterieure segment 20-23 mm × 11-14 mm, reguit. posterieur-laterale 14-18 mm × 7-12 mm, spreidend, die drie anterieure segmente 11-15 mm × 6-8 mm, met die mediane effens langer as die twee weerskante, spreidend. Helmdrade 28-35 mm lank; helmknoppe 6-9 mm lank, donkerpers, reikend tot bo die helfte van die topsegment. Styl 4,5-6 cm lank, rooi, die styltakke 4-5 mm lank; stempels 1,5 mm lank, 2-3 mm breed, rooi, reikend tot naby die punt van die topsegment. Doosvrugte 15-20 mm lank of langer.

KAAPLAND-3318 (Kaapstad): Jonkershoek (-DD); s. koll., s.n. (STE).

—3320 (Montagu): Drew, naby Bonnievale (-CC), *Husling & Niel s.n.* (BOL); Kliprandjie, Sarasrivier naby Ashton, *De Vos 2313* (STE).

—3419 (Caledon): Caledon (-AB), Barnard BOL 30895; 16 ml O van Caledon (-BA), Theron 2022 (PRE); 21 km O van Caledon, Hiemstra 317 (NBG); Botrivier (-AA), Guthrie BOL 30899; Naby Riviersonderend (-BB), Barker 10617 (NBG); Tussen Hartbeesrivier en Agtvallei (-AD), Zeyher 3976 (K); Tussen . . . ? en Hartbeesrivier, Zeyher 39764 (K).

—3420 (Bredasdorp): Naby Swellendam (-AB), *Van der Merwe* BOL 30897, 30898; Naby Heidelberg (-BB), *Barker 5571* (BOL, NBG); Tussen Swellendam en Heidelberg (-BA-BB), *Van Niekerk 442* (BOL); Tussen Swellendam en Riviersonderend (-AA), *De Vos 2311* (STE).

—3421 (Riversdale): Naby Riversdale (-AB), Loubser 998 (NBG), Muir 3249 (BOL), Fergusson BOL 30896; Suid van Riversdale, Wurts 1672 (NBG); Tussen Heidelberg en Riversdale (-AA), Van Breda 2134 (PRE); Heuwels agter Albertinia, suide hang (-BA), Muir 1348 (BOL, SAM).

-3422 (Mosselbaai): Mosselbaai (-AA), Marloth 7451 (PRE).

Sonder vindplek: C.B.S.; Zeyher 3976 (G). Kölbing pl. capens. 16 (G). Caledon wildeblommeskou: BOL 14953.

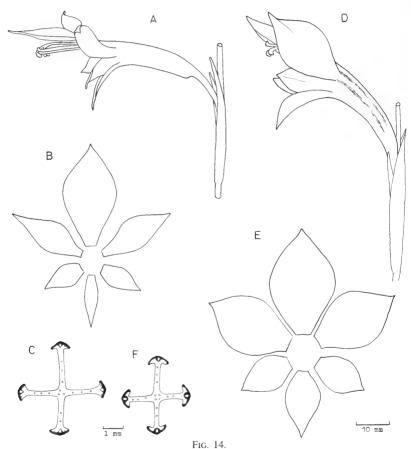
Blomperiode Mei tot September, waarskynlik afhangende van die reëns.

H. muirii kom hoofsaaklik voor in die suidkusdistrikte van Kaapland vanaf Caledon tot Mosselbaai. Dit verskil van die ander Homoglossum-spesies, behalwe H. watsonium, in sy harde, verhoute knoltunicae wat in breë slippe splits en na bo ongesplits en glad is. Van H. watsonium verskil dit in sy geografiese verspreiding, in die bou van die lang loofblaar wat in die droë toestand byna

tereet is maar vier ewe breë sklerenchiemribbe en vier smal, diep, diagonaal geplaasde lengtegroewe het, asook in die perigonium: die segmente is korter en proporsioneel breër en is slegs een-kwart tot een-derde die lengte van die blomdekbuis, en meestal ook korter as die boonste silindriese deel van die buis.

3. SEKSIE QUADRANGULIFOLIUM De Vos sect. nov.

Folium basilare tenue, quadrialatum vel quadrangulatum. Tunicae cormi in fibrillis filiformibus e basi fissae.



A-C, Homoglossum quadrangulare: A, blom; B, perigoniumsegmente; C, dwarssnee deur blaar. D-F, Homoglossum huttonii: D, blom; E, perigoniumsegmente; F, dwarssnee van blaar.

Typus sectionis: H. quadrangulare (Burm.f.) N.E.Br.

Die seksie word gekenmerk deurdat die lang smal basale blaar 'n vier-vleuelige lamina het met 'n sterk, breë rif op die rand van elke vleuel, en deur membraneuse of effens verhoute knoltunicae wat vanaf die knolbasis gesplits is in smal filiforme, of soms elsvormige, gebuigde fibrille minder as 1 mm breed. In die boonste helfte is die tunicae nie opgesplits nie en het hulle 'n opgehewe arenetwerk op hul oppervlakte sigbaar.

Die anatomiese bou van die lamina van die basale loofblaar is identies by die vier spesies. Die enigste are wat van buite sigbaar is, is dié op die rande van die vier vleuels, geleë in 'n laag subepidermale sklerenchiem. Die ander are is diep in die mesofil ingebed. In elke vleuel lê verlengde mesofilselle met hul lang asse parallel met die epidermis.

7. Homoglossum quadrangulare (Burm.f.) N. E. Brown in Trans. R. Soc. S. Afr. **20:** 279 (1932); Delpierre & Du Plessis 1973 p. 76.

Antholyza quadrangularis Burman f. 1768 p. 1, basionym; Houttuyn 1780 p. 63; Vahl 1805 p. 123; N. E. Brown 1929 p. 131; Klatt 1863 p. 727 pro syn. & 1895 p. 288 pro syn.; non Baker 1877, 1892, 1896.

Gladiolus quadrangularis (Burm.f.) Aiton 1810 p. 97 pro parte, excl. syn. Ker & Andr.; Steudel 1840 p. 106; non Ker 1802, 1805, 1827, nec Sprengel 1825. Icones: Delpierre & Du Plessis Fig. 81; die huidige werk Fig. 14A-C.

Holotipe: Burman s.n. in Hb. Burman in G.

Plante 50-90 cm hoog. Knol 1,5-3 cm in deursnee, tunicae van onder tot die middel gesplits in parallelle filiforme fibrille, in die boonste helfte ongesplits met 'n opgehewe arenetwerk. Stingel 50-80 cm hoog. Laagteblare meestal 2, 2-12 cm lank. Loofblare meestal 3, naak, die basale blaar korter as die bloeistingel of soms langer, met 'n 10-40 cm lange, na bo geribde blaarskede en 'n unifasiale lamina 20-60 cm lank, tot 4 mm breed, kruisvormig in dwarssnee met 4 ewe breë vleuels en sterk ribbe op hul rande, soms pseudo-tereet na die top met vier groewe; die tweede blaar met 'n langer blaarskede en 'n 5-10 cm lange lamina waarvan die top soos die eerste s'n is; die derde blaar 3-13 cm lank, toegerol, soms half-verberg onder die tweede. Aar onvertak, met 3-7 of soms tot 10 blomme na die een kant gedraai, soms met 'n golwende of horisontaal gebuigde rachis. Bractea smal-eiervormig, rooigroen, 22-40 mm lank, stomp. Bracteola effens korter as die bractea, soms verberg onder die bractea. Blom 6,5-8,5 cm lank, helder kersierooi (RHS 41B, 42B, 43B, 45C) tot ligrooi, soms pienk of appelkooskleurig, die anterieure segmente soms ligter, effens geel in die keel. Perigoniumbuis met die smal basale gedeelte 13-15 mm lank, met 'n klein nektarsakkie waar dit skielik verbreed, en met die boonste silindriese deel 20-25 mm lank of soms tot 30 mm, 6-7 mm in deursnee; segmente eiervormig tot smal-eiervormig of omgekeerd-smal-eiervormig, akuminaat of skerp, die topmediane (posterieure) segment 20-30 mm × 12-16 mm; top-laterale segmente

effens teruggebuig, $18-22 \text{ mm} \times 6-9$; die drie anterieure segmente spreidend en teruggebuig, $9-18 \text{ mm} \times 3-8 \text{ mm}$, met die mediane segment effens smaller en langer as die twee weerskante, of net so lank. Helmdrade 25-40 mm lank; helmknoppe 9-15 mm lank, nie-apikulaat, die toppe na agter gebuig, liggeel, dikwels met 'n smal pienk streep waar die thecae oopsplits, reikend vanaf die helfte tot naby die top van die posterieure segment. Vrugbeginsel 5-8 mm lank, subsessiel; styl 5,5-6,5 cm lank, liggeel, die styltakke 4-6 mm lank, rooierig; stempels 1,5 mm lank, 2-3 mm breed, rooi. Doosvrugte smalomgekeerd-eiervormig, $20-30 \text{ mm} \times 7 \text{ mm}$.

KAAPLAND—3219 (Wupperthal): Boplaas, Koue Bokkeveld (-CD), *Jackson s.n.* (NBG); Naby De Keur, Koue Bokkeveld, *Loubser 2018* (NBG).

—3319 (Worcester): Ceres (-AD), *Marloth 8793* (PRE); Prince Alfred's Hamlet, *Lewis 2664* (SAM); Gydouw (-AB), *Leipoldt 3048* (BOL); Gydouwpas, *Leighton* BOL *30892* (BOL); Leeufontein (-AD), *De Vos 2303* (STE); Westelike voet van Theronsbergpas (-BC), *De Vos 2304* (STE); Westelike hange van Theronsbergpas, *Goldblatt 545* (BOL); Hottentotskloof, *Barker 1545*, *3032* (NBG), *Acocks 23759* (PRE); Koo, aan die voet van Naudésberg (-DB), *Lewis 6056* (NBG, STE).

Sonder bepaalde vindplek: *Hb. Burman* (G). Ceres wilde-blommeskou: BOL 30893, 20314, SAM 60117. Kaapstadse blommeskou, ex Ceres: BOL 30894, 14279. Kaapstadse blommeskou: *Marloth* 8793 (PRE, STE).

Blomtyd: Augustus tot Oktober.

Hierdie spesie het sy distribusiesentrum in die Ceres-distrik en kom voor beide in die Warm-Bokkeveld met 'n hoogte van laer as 450 meter en in die Koue-Bokkeveld wat 1 000 tot 1 200 meter bo seespieël lê. Dit word gekenmerk deur filiforme knolfibrille, 'n vier-vleuelige basale loofblaar met 'n papilleuse interkostale epidermis en met verspreide reusagtig groot epidermisselle op die vleuelrande waar daar dikwels haarstompies in rye ontstaan; verder deur blomme met 'n klein nektarsakkie waar die blomdekbuis verbreed en met skerp of akuminate blomdeksegmente, die drie onderste segmente spreidend en teruggebuig en nagenoeg ewe groot (of die mediane effens langer en smaller), en min of meer die helfte so groot as die posterieure segment. Heelwat variasie kom voor in die kleur en die vorm van die perigoniumsegmente.

Daar is verwarring gewees oor hierdie spesie vanaf sy ontdekking meer as twee honderd jaar gelede, tot 1929. Linnaeus het dit geken, want in sy herbarium is 'n eksemplaar daarvan, LINN 60.4, met sy identifikasie, *A. aethiopica*, daarby, asook Smith se kommentaar: "non aethiopica. nervosa?". Volgens 'n private mededling van prof. T. T. Barnard wat die korrespondensie van Linnaeus, die Burmans en D. van Royen bestudeer, is hierdie eksemplaar ongetwyfeld een wat David van Royen in Maart 1763 aan Linnaeus gestuur het en beskryf het onder *Antholyza? capensis* in sy manuskrip, *Centuria observationum et quaestionum botanicarum*. Sy noukeurige beskrywing pas besonder goed op die eksemplaar LINN 60.4, o.a. dat die stingel "procumbens" is. In die kantlyn van die manuskrip het

Linnaeus aangeteken, net soos op die eksemplaar, "Anthol. aethiopica". Volgens die bogenoemde korrespondensie tussen Linnaeus en Burman, het Linnaeus egter later besluit dat die plant verwys moes word na Gladiolus tristis.

Waarskynlik omdat die basale loofblare van die twee spesies, *H. quadrangulare* en *H. abbreviatum*, eenders is, het Ker (1802) 'n plant geïllustreer in Curtis's se bot. Mag. t. 567 (nou *H. abbreviatum*), gelyk gestel aan Burman se *Antholyza quandrangularis*, sonder dat hy die Burman-tipe in G gesien het. Vir die volgende meer as hondered jaar is Ker se plant as identies met Burman s'n beskou, bv. deur Baker (1896), totdat N. E. Brown (1929) ontdek het dat Burman se tipe van Ker se plant verskil. Die huidige herondersoek van Burman se tipe bevestig Brown se sienswyse.

- 8. **Homoglossum huttonii** N.E.Br. in Trans. R. Soc. S. Afr. **20:** 278 (1932); L. Bolus 1933 p. 46.
- H. hollandii L. Bolus p. 47—syntypi Holland 3617 & BOL 20077 in BOL; Courtenay-Latimer e.a. 1967 pl. 16,3; Gledhill 1971 p. 90.
- H. hollandii L. Bol. var. zitzikammense L. Bolus 1933 p. 47—holotypus Fourcade 59 in BOL; Batten & Bokelmann 1966 p. 42.

Icones: S. Afr. Gard. & Country Life **23:** 46 Fig. D; Courtenay-Latimer *e.a.* Pl. 16 Fig. 3; Batten & Bokelmann 1966 Pl. 33 Fig. 5; Gledhill 1971 Pl. 16 Fig. 7; die huidige werk Fig. 14D-F.

Holotipe: Hutton s.n. in K.

Plante 25 -85 cm hoog. Knol 1,5-2,5 cm in deursnee, met die tunicae tot bo die middel gesplits in sterk, krom, elsvormige fibrille 0,5-0,8 mm dik, en na bo dikwels ongesplits met 'n opgehewe arenetwerk. Stingel 25-75 cm lank, 1-2,5 mm in deursnee onder die aar. Laagteblare 2, 2-8 cm lank. Loofblare 3, naak, die basale blaar so lank soos die stingel of soms korter of langer, met die lang, fyn geribde blaarskede 10-22 cm lank en die lamina 20-60 cm of soms net 10 cm lank, 1-4 mm breed, kruisvormig in dwarssnee, met 4 ewe breë vleuels met 'n sterk rib op die rand van elke vleuel, of soms in die droë toestand pseudotereet met byna geslote groewe; die tweede blaar grootliks skedevormend met 'n lamina 2-8 cm lank, aan die top soos die eerste; die derde blaar 4-7 cm lank, soms half verberg onder die tweede blaar. Aar onvertak, met 2-7 blomme eensydig gedraai, of soms met slegs één blom, die rachis soms effens golwend. Bractea groen of rooigroen, 25-50 mm lank, stomp, soms klein-apikulaat, effens langer as die smal deel van die blomdekbuis. Bracteola effens korter as die bractea, dikwels verberg onder die bractea. Blomme 7-10,5 cm lank, stygend, effens gebuig, op 'n 2 mm lange pedisel. Perigoniumbuis met die smal basale gedeelte 20-30 mm lank, die silindriese boonste gedeelte effens gebuig, 25-30 mm lank, 5-8 mm in deursnee, met 'n donkerrooi lengtestreep onder elke sinus van die top-laterale segmente, sonder 'n duidelike nektarsakkie; segmente ellipties tot breed ellipties of omgekeerd eiervormig, skerp of akuminaat, die posterieure segmente rooi of oranjerooi

(RHS 35A, 34C), die anterieure segmente spreidend of effens teruggebuig, geel, oranjegeel of rooi met 'n geel keel; die top-mediane segment 28–38 mm × 15–22 mm, reguit, top-laterale 25–30 mm × 10–18 mm, spreidend, die drie anterieure segmente 10–22 mm × 6–12 mm, met die mediane segment effens smaller en soms effens langer as die twee weerskante. *Helmdrade* 3,5–4,5 cm lank; *helmknoppe* 8–10 mm lank, stomp, geel met 'n pienk streep waar hulle oopsplits. *Styl* 6,5–8 cm lank, die styltakke 2,5–3 mm lank; *stempels* 2 mm lank, 2 tot byna 4 mm breed, ligrooi, reikend laer tot hoër as die top van die posterieure segment. *Doosvrugte* 25–30 mm lank of nog langer.

Volksname: rooi aandblom, rooi afrikaner, East Cape flame.

KAAPLAND—3323 (Willowmore): Nature's Valley (-DC), *De Vos 2291* (STE), *Liversedge Pl. 16 no. 3* (PRE), *Immelman 86* (NBG); Grootrivier-mond, *Keet 537* (STE).

- —3325 (Port Elizabeth): Uitenhage (-CD), Bokelmann 1 Pl. 20 (NBG); Grasveld naby Swartkopsrivier (-DC), Ecklon & Zeyher 141 (PRE); Naby Port Elizabeth, Pappe SAM 21502, Hammer SAM 9552, Cory BOL 30904, West (K), West 6 (GRA); St. Albans 'n paar myl NW van Green Bushes (-CD), Holland 3617 (BOL, K); Bethelsdorp, L. Bolus 20077 (BOL, PRE, SAM, K), King GRA 1884; Na Witteklip, Rodin 1050 (BOL, K); Theescombe, Urton s.n. (NBG); Redhouse (-DC), Paterson 660 (BOL); Bakensrivier, Fries, Norlindh & Weimarck 486 (SAM); Kaapse pad, 14de myl van P.E. (-CD), Long 659 (GRA, PRE, K); Kaapse pad, Denman 260 (GRA); Kabega, Urton 275 (GRA); Algoa Bay (-DC-DD), MacWilliam s.n. (G); Krakakamma & Van Stadensberg (-CC), Drège Irid. 154 (G).
- —3326 (Grahamstown): Naby Grahamstown (-BC), Guthrie 3326 (BOL), Bolton (K), MacOwan (K), Thomas (NBG); Broekhuizenspoort naby Grahamstown, Galpin 66 (K); Highlands (-AD), Daly & Sole 298 (GRA, PRE), Bayliss 2318 (NBG); Slaaikraal, Hoole GRA 1881; Coldspring, Britten GRA 1883, Coetzee GRA 1879; Coldstream (-BC), Galpin 66 (GRA, PRE); Albany District, Hulton (K).
- -3327 (Peddie): Oos-Londen (-BB), Mason (K).
- —3423 (Knysna): Plettenbergbaai (-AB), *Rogers 26713* (PRE); Oop vlakte, Ratelsbos, *Fourcade 59* (BOL, GRA); Bo Stormsriviermond (-BB), *Acocks 21290* (NBG, PRE, K), *Wurts 2131* (NBG); Langs pad na Stormsriviermond, *De Vos 2292* (STE).
- —3424 (Humansdorp): Humansdorp (-BB), Loubser 896 (NBG); Swartsrivier tussen Humansdorp en Jeffreysbaai, Fourcade 4006 (K); Oos van Humansdorp, Sidey 1687 (PRE), Urton 192 (GRA); Witelsrivier (-AA), MacPherson & Boulle 14 (NBG).

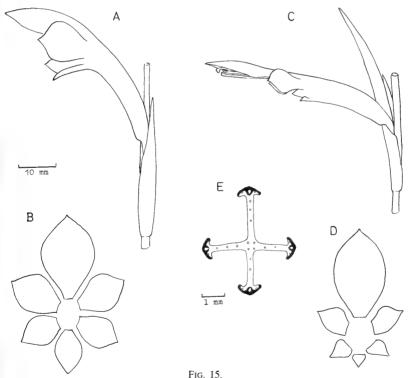
Oosgrens sonder nadere gegewens: Barber (K).

Blomtyd Junie tot September.

L. Bolus het nie die tipe van H. huttonii gesien nie. Sy meld by haar

beskrywing van *H. hollandii* dat die laasgenoemde baie naby *H. huttonii* is, maar dat dit, volgens die beskrywing van *H. huttonii*, onderskei word deur die baie langer blomdekbuis in vergelyking met die segmente en deur die breër en korter onderste segmente; verder dat die blomdekbuis dikwels byna reguit is. Haar variëteit *zitzikammense* word gekenmerk deur groter, meer robuste plante met meer blomme. Daar is nou egter soveel tussenvorms gekry wat *H. huttonii* (van Grahamstad tot Oos-Londen) met *H. hollandii* (van Port Elizabeth) en *H. hollandii* var. *zitzikammense* (van die Tsitsikamma en Knysna) verbind, dat hulle slegs as geografiese vorms van een spesie beskou moet word.

Variasie kom voor in die grootte en aantal van die blomme, die breedte van die blomdeksegmente, asook in die breedte van die knoltunicafibrille, wat wissel van minder as 0,5 mm tot byna 1 mm.



A-B, Homoglossum fourcadei: A, blom; B, perigoniumsegmente. C-E, Homoglossum abbreviatum: C, blom; D, perigoniumsegmente; E, dwarssnee deur blaar.

H. huttonii staan naaste aan H. fourcadei waarvan dit onderskei word veral aan die donkerrooi lengtestrepe op die boonste deel van die perigoniumbuis reg onder die sinusse van die top-laterale segmente.

9. Homoglossum fourcadei (L. Bol.) N.E.Br. in Trans. R. Soc. S. Afr. **20:** 279 (1932).

Antholyza fourcadei L. Bolus 1927 p. 117, basionym.

Fig. 15A-B.

Holotipe: Fourcade 2337 van naby Humansdorp in BOL. Isotipe in NBG.

Plante 50 cm tot meer as 1 m hoog. Knol 1-2 cm in deursnee, tunicae membraneus, gesplits in baie fyn filiforme gebuigde parallelle fibrille tot bo die middel, in die boonste deel dikwels ongesplits en met 'n opgehewe arenetwerk. Stingel 50 tot meer as 100 cm lank. Laagteblare 2, tot 12 cm lank. Loofblare 3, naak, die basale blaar 50-120 cm lank, langer as die bloeistingel, met die geribde skede 20-30 cm lank en die unifasiale lamina 40-90 cm lank, 2-4 mm wyd, kruisvormig in dwarssnee, die vier vleuels ewe breed met 'n breë, sterk rib op elke rand, na bo pseudotereet, smaller, met byna geslote groewe; die tweede blaar met die lamina 8-12 cm lank, met slegs die punt soos by die eerste; die derde blaar 4-10 cm lank met 'n baie kort lamina. Aar onvertak, met 3-7 eensydige blomme, die rachis soms effens golwend. Bractea smal-eiervormig, groen of rooigroen, stomp, 3-5 cm lank. Bracteola korter as die bractea. Blomme 6,5-8 cm lank, effens gebuig, min of meer stygend, rooi of groengeel en die posterieure segmente met rooi of gryspers are. Perigoniumbuis met die smal basale gedeelte 15-20 mm lank, gebuig waar dit skielik verbreed en met 'n sakkie, die silindriese boonste gedeelte 20-30 mm lank, 5-6 mm in deursnee; segmente breedeiervormig tot byna rond maar wigvormig aan die basis en skerp tot akuminaat, die posterieure segment reguit, 16-25 mm × 12-15 mm; top-laterale segmente 12-15 mm × 9-12 mm, spreidend; die drie anterieure segmente kleiner, spreidend, onder-laterale 6-12 mm × 6-8 mm, onder-mediane 6-9 mm × 5-7 mm. Helmdrade 2,5-3,5 cm lank; helmknoppe 9-12 mm lank. Styl 5-6 cm lank, styltakke 4-5 mm lank, dikwels rooierig; stempels 2 mm lank, 2 mm breed, rooierig, soms hoër as die top van die agterste blomdeksegment geleë.

KAAPLAND—3322 (Oudtshoorn): Naby Herold (-CD), PRE 32581; Naby Molenrivier tussen Avontuur en Montagupas (-DD), Gillett 1611 (BOL, K); Langkloof (-DB), Fourcade 1717 (BOL).

—3323 (Willowmore): Uniondale (-CA), Fourcade SAM 25876, Lovegrove s.n. (NBG); Headwaters of Wagenboomsrivier, Fourcade 2337 (BOL).

—3423 (Knysna): Rotshange bo die see tussen Knysna-Hoofde en Noetzi (-AA), *Thomas s.n.* (NBG).

—3424 (Humansdorp): Naby Humansdorp (-BA/BB), *Fourcade 2337* (BOL). Sonder nadere vindplek: Kaapstadse blommeskou: *Marloth 8846* (STE). Blomperiode September tot November.

Hierdie spesie, hoofsaaklik van die Klein-Karoo en die suidkusdistrikte van Knysna en Willowmore, staan morfologies, asook min of meer geografies, intermediêr tussen *H. huttonii* en *H. abbreviatum*. Dit verskil van *H. huttonii* in sy effens kleiner blom met die segmente in die droë toestand donkerder rooi met duidelike ligte of donker are, en die blomdekbuis met 'n nektarsakkie en sonder die donkerrooi lengtestrepe onder die sinusse van die laterale segmente. Van *H. abbreviatum* verskil dit in sy effens groter anterieure blomdeksegmente wat in die droë toestand ligter gekleur is en wat ongeveer op dieselfde hoogte as die posterieure segmente vanuit die blomdekbuis afkomstig is; ook in sy later blomperiode (September tot November in teenstelling met Mei tot September by *H. abbreviatum*.

Dit is skynbaar taamlik skaars en is nie in die nabye verlede weer gevind nie.

10. **Homoglossum abbreviatum** (Andr.) Goldblatt in J1 S. Afr. Bot. **37:** 443, 408 (1971); Delpierre & Du Plessis 1973 p. 40.

Gladiolus abbreviatus Andrews 1801 t. 166, basionym, iconotypus.

Antholyza abbreviata (Andr.) Persoon 1805 p. 42; N. E. Brown 1929 p. 131.

Petamenes abbreviatus (Andr.) N. E. Brown 1932 p. 276; L. Bolus 1933 p. 46; Goldblatt 1971 p. 408 pro syn.; Lewis e.a. 1972 p. 299.

Gladiolus quadrangularis sensu Ker 1802 t. 567 & 1805 p. 230 & 1827 p. 131, excl. syn. Burm.; sensu Aiton 1810 p. 97 pro parte, excl. syn. Burm.; sensu Roemer & Schultes 1817 p. 411; sensu Sprengel 1825 p. 151, excl. syn. Vahl; non Steudel.

Petamenes quadrangularis (Ker) Salisbury 1812 p. 324; Sweet 1830 p. 500; Loudon 1841 p. 42, excl. svn. Burm.

Anisanthus quadrangularis (Ker) Sweet 1827 p. 397; Klatt 1863 p. 727, excl. syn. Burm., & 1882 p. 344 pro parte, & 1895 p. 228, excl. syn. Burm.

Antholyza quadrangularis sensu Baker 1877 p. 179 & 1892 p. 231 & 1896 p. 166; non Burm. 1768, nec Houttuyn 1780, nec Brown 1929.

Icones: Andrews 1801 t. 166; Curtis's bot. Mag. t. 567; S. Afr. Gard. & Country Life **23:** 46 Fig. F (1933); Goldblatt 1971 p. 407 Fig. 24, i; Delpierre & Du Plessis 1973 Fig. 46; die huidige werk Fig. 15C-E.

Iconotypus: Andrews, Bot. Rep. t. 166.

Plante 30–65 cm hoog. Knol 1–2 cm in deursnee, met effens verhoute tunicae wat vanaf die basis gesplits is in smal parallelle fibrille en in die boonste helfte ongesplits is met 'n opgehewe arenetwerk. Stingel 30–65 cm lank, sterk. Laagteblare 2, tot 10 cm lank. Loofblare 3, selde 4, naak, dikwels spirodistieg, die basale blaar korter tot langer as die stingel, soms met 'n effense spiralige torsie, met die blaarskede 10–20 cm lank en die unifasiale lamina 20–40 cm lank, 1,5–5 mm breed, akuminaat, kruisvormig in dwarssnee, die vier vleuels nagenoeg ewe breed, met 'n sterk rib op elke rand, na bo dikwels pseudotereet met byna geslote groewe; die tweede blaar met die blaarskede breed, 30–40 cm lank, en die lamina 4–20 cm lank, met slegs die top unifasiaal en pseudotereet; die derde blaar tot 7

cm lank, bifasiaal, dikwels onder die tweede verberg. Aar onvertak, selde vertak, met 3-8 blomme, die rachis tot 3 mm in deursnee, die blomme min of meer eensydig of in twee rye met 'n hoek van tot 60° tussenin. Bractea 4.5–7 cm lank. rooi, pienk of oranje, stomp, baie langer as die perigoniumbuis. Bracteola korter as die bractea, vaal-pienk, grootliks verberg deur die bractea. Blomme 5,5-9 cm lank, effens gebuig, nagenoeg stygend, rooi, donkerrooi, bruinrooi of oranierooi (RHS 47A, B, 50A, 39A, 35A), die anterieure segmente swartgroen na die basis en geelgroen na bo en om die rande. Perigoniumbuis met die smal basale deel 18-28 mm lank, tot 3 mm in deursnee, met 'n klein nektarsakkie waar die buis verbreed, en met die silindriese boonste deel 20-28 mm lank, 6-8 mm in deursnee; segmente baie verskillend in grootte, die posterieure segment die grootste, ejervormig, konkaaf, reguit, halfstomp tot skerp of apikulaat, half deurskynend, 22–28 mm × 13–15 mm; lateraal-posterieure segmente skeefromboïed, met die anterieure helftes kleiner as die posterieure helftes, reguit, skerp of akuminaat, 8-10 mm × 7-8 mm; die drie anterieure segmente baie klein, nagenoeg driehoekig, skerp of akuminaat, effens spreidend, laer as die ander aan die blomdekbuis vasgeheg, met die laterale segmente 4-6 mm × 3-5 mm en die mediane 2-4 mm × 2-4 mm. Helmdrade 3-4 cm lank; helmknoppe 9-13 mm lank, ligrooi of donker persooi, reikend 5 mm laer as die top of tot by die top van die posterieure segment. Stvl 5-7 cm lank, ligrooi, styltakke 4-5 mm lank; stempels lig- tot donkerrooi, 1,5 mm lank, tot 3 mm breed, later reikend tot die top van die posterieure segment. Doosvrug smal-ellipsoïed, skerp aan die top en basis, 2.5-3 cm lank.

KAAPLAND—3319 (Worcester): Breerivier (-CB-DD), *Leipoldt* BOL 18539 (BOL, PRE, SAM).

—3320 (Montagu): Sarasrivier, Ashton, naby klein stroompie (-CC), *Lotz s.n.* 17.8.70 (STE).

—3419 (Caledon): Stokoe BOL 17454; Botrivier (-AA), Walters 15 (NBG); Botrivier—Caledon (-AA-AB), Barker 7334 (NBG); Botrivier—Swellendam (-BA-BB), Loubser 2001 (NBG); Riviersonderend (-BB), Pattison Aug. 1916 (BOL); 6 ml W van Riviersonderend, Thomas s.n. (NBG); 9 ml W van Riviersonderend (-BA), Marais NBG 505/60; 3–5 ml O van Botrivier (-AB), De Vos 2310 (STE); Eseljagt, tussen Caledon en Villiersdorp, Barnard NBG 2315/32 (BOL); Tussen Caledon en Napier (-BC), Esterhuysen 3057 (BOL); 12 ml van Botrivier na Grabouw (-AA), Goldblatt 292 (BOL).

—3420 (Bredasdorp): Swellendam (-AB), *Pappe* SAM 21501; Wydgelegen (-AD), *Barker 4545* (BOL, NBG).

—3421 (Riversdale): Riversdale (-AB), *Marloth 11251* (PRE); 9 ml W van Riversdale (-AA), *Marais* NBG 505/60 (STE); Palmyra, Heidelberg, *Loubser 2152* (NBG), *De Vos 2305* (STE).

S.W. streek, sonder nadere gegewens: *Guthrie* Aug. 1917 (BOL). Blomperiode Mei tot September.

Hierdie spesie is maklik van ander *Homoglossum*-spesies onderskeibaar aan sy blomme met die top-mediane segment baie groot en die drie anterieure segmente besonder klein, dikwels swartgroen met geelgroen rande en op verskillende hoogtes in die blomdekbuis ingeplant. Dit is die laaste stap van die progressiewe grootte-verskille tussen die posterieure blomdeksegment en die anterieure segmente en dit kan as die hoogste gespesialiseerd van die *Homoglossum*-spesies beskou word.

Sy naaste verwant is *H. fourcadei* wat die drie anterieure segmente effens groter en pienker het en min of meer op dieselfde hoogte vasgeheg aan die blomdekbuis, en 'n effens later blomperiode het.

N. E. Brown het, na 'n studie van die Iridaceae in die Burman-herbarium, gevind (1932 p. 256) dat Ker die plant wat geïllustreer is in die Curtis's bot. Mag. t. 567 (1802), asook Andrews (1801) se Gladiolus abbreviatus, verkeerdelik geïdentifiseer het as dieselfde as Burman se Antholyza quadrangularis (wat Ker nooit gesien het nie en wat slegs in sy 4-vleuelige blaar met die eersgenoemde ooreenstem). Hierna is die twee spesies keer op keer verenig. Salisbury (1812) het Ker en Andrews se plante in sy nuwe genus Petamenes as P. quadrangularis geplaas, en Sweet (1827) in sy genus Anisanthus. In 1932 besorg N. E. Brown aan die spesie weer sy korrekte epiteton abbreviatus terug, maar behou dit onder Petamenes. In 'n ongepubliseerde aantekening in die Bolus-herbarium verklaar Lewis dat sy nie kan insien waarom mnr. N. E. Brown Petamenes en Homoglossum twee aparte genera maak nie en dat die enigste verskil skynbaar is dat by Petamenes die blomdeklobbe "unequal" is, terwyl hulle by Homoglossum "subequal or not very unequal" is. Na 'n ondersoek van die kariotipes, plaas Goldblatt (1971) P. abbreviatus oor na Homoglossum, P. buckerveldtii na Gladiolus en die ander Petamenes spesies na Oenostachys.

UITGESLUITE SPESIES

Homoglossum aureum (Bak.) Obermeyer in Lewis e.a. 1972 p. 299. Dit is Gladiolus aureus Baker in Fl. Cap. 6: 530 (1896); Lewis 1950 p. 257; Marais 1965 sub t. 479; Goldblatt 1971 p. 408, Fig. 24c—holotypus Fair BOL 7951 in K, isotypi in BOL, GRA, PRE, B, Z. Die boonste deel van die perigoniumbuis is tregtervormig. Omdat hierdie kenmerk tipies is vir die genus Gladiolus, word die spesie terug geplaas na Gladiolus. (As dit in Homoglossum opgeneem word, sal dit 'n uitsondering wees op een van die belangrikste kenmerke van hierdie genus, te wete die byna silindervormige boonste helfte van die perigoniumbuis.)

H. caryophyllaceum (Burm.f.) N. E. Brown 1932 p. 279. Dit is Gladiolus caryophyllaceus (Burm.f.) Poir. in Lam. Encyc. Suppl. 2: 795 (1812); Lewis e.a. 1972 p. 114. Syn. Antholyza caryophyllacea Burm.f. 1786 p. 1, basionym—holotypus Burman s.n. in G.

H. lucidor (L.f.) Baker 1877 p. 161. Dit is Anapalina triticea (Burm.f.) N. E.

Brown 1932 p. 275; Lewis 1960 p. 54; Lewis e.a. 1972 p. 301. Syn. Gladiolus lucidor (L.f.) Baker 1892 p. 227.

H. macrosyphon Schlechter ined. in herb. (Schlechter 10136). Dit is Tritoniopsis nervosa (Bak.) Lewis 1959 p. 351. Hierdie eksemplaar is ook die tipe van Tanaeosolen nudus N. E. Brown 1932 p. 262 wat Lewis (1959) as 'n sinoniem van Tritoniopsis nervosa siteer.

H. pulchrum (Bak.) Schlechter 1898 p. 453. Dit is Anapalina pulchra (Bak.)
N. E. Brown 1932 p. 275; Lewis 1960 p. 59. Syn. Antholyza pulchra Baker 1896
p. 531, basionym—holotypus Schlechter 7611 in K, isotypi in BOL en PRE.

Antholyza (Homoglossum) schlechteri Baker 1904 p. 1007 is Gladiolus natalensis (Eckl.) Reinw. ex Hooker in Curtis's bot. Mag. sub t. 3084 (1831); Lewis e.a. 1972 p. 44.

BEDANKING

My opregte dank gaan eerstens aan die hoofde van die volgende herbaria vir die uitleen van *Homoglossum*-materiaal en veral hul tipe-eksemplare waarsonder die ondersoek nie gedoen sou kon word nie: die Bolus-herbarium van die Universiteit van Kaapstad (BOL), Compton- en S. Afrikaanse Museum-herbaria te Kirstenbosch (NBG en SAM), Nasionale herbarium, Pretoria (PRE), en sy takke te Stellenbosch (STE) en Grahamstad (GRA), die herbaria van die Royal Botanic Gardens, Kew (K), Botanischer Garten und botanisches Museum, Berlin-Dahlem (B), en Conservatoire et Jardin botaniques, Genève (G);

tweedens aan prof. T. T. Barnard vir sy waardevolle inligting oor sekere spesies;

derdens aan die talle mense wat met die versameling van vars materiaal gehelp het, veral prof. Elsabe Malan, mej. Anna Uys, mev. A. E. Cillié en mnr. O. P. H. Augustyn van Stellenbosch, mnr. en mev. E. M. Davidson van Palmyra, Heidelberg, Kaap, mnr. L. Mostert van Romansrivier, Wolseley, en mnr. J. W. Loubser en prof. G. R. Delpierre van Bellville;

en laastens aan die tegniese personeel en mev. J. M. Serdyn van die Botanie-departement alhier wat op vele maniere behulpsaam was.

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A NEW SPECIES OF *EUCOMIS* L'HERIT. (LILIACEAE) FROM SOUTH AFRICA

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ABSTRACT

A new species of Eucomis L'Hérit. from the Drakensberg of Natal and Lesotho and mountains of the Eastern Cape is described.

UITTREKSEL

'N NUWE EUCOMIS-SOORT (LILIAECEAE) VAN SUID-AFRIKA

'n Nuwe soort van Eucomis L'Herit. van die Drakensberge van Natal en berge van die Oos-Kaap word beskryf.

Introduction

During a taxonomic study of the South African representatives of the genus *Eucomis* L'Hérit. it became clear that *Eucomis regia* (L.) L'Hérit. previously known as *E. nana* (Burm.f.) L'Hérit. (Reyneke, 1974) is confined to the South Western Cape Province. Specimens from Natal, Lesotho and the Eastern Cape Province previously named *E. regia* did not agree with either *E. regia* or any other described species, and are here described as a new species. This brings the total number of *Eucomis* species to ten of which five are endemic in the Republic of South Africa.

DESCRIPTION.

Eucomis schijffii Reyneke spec. nov. similis E. regiae (L.) L'Hérit., sed distinguitur floribus in scapum non impressis, filamentis ac perigonio purpureis, et quod aestate floret.

Bulb pearshaped to ovoid, surface rough, imbricate. Leaves 3 to 4, seldom more than 4, ovate, without purple spots, not carinated, usually prostrate, lateral veins prominent above as grooves and as dark green stripes below, 60 to 100 (170) mm long and 40 to 70 mm broad, margin smooth or minutely crisped. Inflorescence a raceme or pseudospike, 25 to 30 mm in diameter. Peduncle solitary, club shaped, 20 to 70 mm long, sometimes with purple spots. Flowering part of spike 10 to 20 mm long, seldom with purple spots. Fertile bracts shorter than flowers, sagitate, 2 to 3 mm long and 5 mm broad at base of spike, 8 to 10 mm long and 3 mm broad at apex of inflorescence, young bracts with purple margins, older bracts without purple margins. Coma (viz. sterile bracts at apex of inflorescence) consists of 10 to

Accepted for publication 2nd July, 1976.



Eucomis schijffii Reyneke. A plant from Cathedral Peak collected by P. Vorster of the Botanical Research Institute.

15 bracts, declinate, bracts oval, 15 to 20 mm long and 10 to 20 (25) mm broad. Flowers 10 to 20 in number, close to one another. Pedicles absent or 1 (2) mm long. Perianth segments dark purple, c. 10 mm long and 5 mm broad, fused at the base. Stamens fused with perigone below. Filaments purple, triangular c. 6 mm long. Ovary trilocular, green, slightly purplish below, apically grooved between the three loculi, c. 3 mm long. Style green at base, purple apically, c. 5 mm long. Stigma white. Fruit an inflated, dehiscent capsule, pericarp thin and membranous, purplish. Seeds, axile, c. 5 in each locule, ovate with brown testa.

Flowering from the middle of December to the end of February.

Type: Natal—2829 (Harrismith): Cathedral Peak, Twins Cave (-CC), Vorster 45 (PRE!, holo.).

DISTRIBUTION. See Fig. 2.

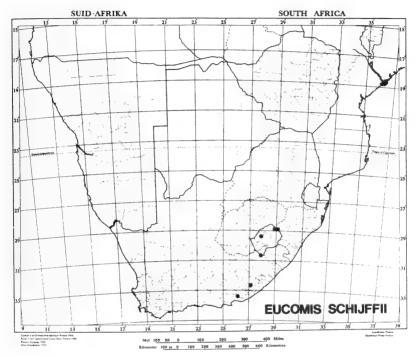


Fig. 2. The known distribution of *Eucomis schijffii* Reyneke.

Drakensberg of Natal and Lesotho and mountains of the Eastern Cape Province of the Republic of South Africa.

NATAL—2828 (Bethlehem): Mont-aux-Sources (-DD), open grassveld, *Bayer & McClean 264* (NU and PRE); The Sentinel, *Steyn 1110* (NBG).

—2829 (Harrismith): Cathedral Peak Forest Station (-CC), *Schelpe 91* (NU), *917* (NH); Twins Cave, *Vorster 45* (PRE!, holo.) *38*, *39*, *42*, *43*, *46*, *47*, *48* (PRE). LESOTHO—2927 (Maseru): Berea (-BD), Mamlapi, in shade along stream,

Marais 1297 (PRE), Compton 21412 (NBG), Jacot Guillarmod 596 (PRE).

-2928 (Marakabei): Maluti Mountains (-AC)?, Dieterlen 1263 (PRE).

CAPE PROVINCE—3027 (Lady Grey): Ben Macdhui (-DB), Doodmanskrans, *Galpin 6869* (PRE).

- -3227 (Stutterheim): Hogsback (-CA), Story s.n. (PRE).
- -3326 (Grahamstown): Alicedale (-AC), Cruden s.n. (GRA).

E. schijffii (Fig. 1) is the smallest of all the Eucomis species and it was formerly placed with E. regia (L.) L'Hérit. It is distinguished inter alia from E. regia, which flowers in the late winter, by flowering in the late summer. It also differs from the former species in that the perigone and filaments are coloured a vivid purple and that the flowers are not sunken into the scape. The perigone of E. regia is green with a purplish appearance at the base and margin, while the filaments are green and the flowers sunken into the scape.

The author takes great pleasure in naming this species *Eucomis schijffii* in recognition of the valuable contribution which Professor H. P. van der Schijff has rendered to the study of the morphology of South African plants.

ACKNOWLEDGEMENTS

The author wishes to express his sincere gratitude to the Research and Publications Committee of the University of Pretoria and the C.S.I.R. for financial aid provided. Thanks are also due to Mrs A. A. Mauve (Obermeyer) and Mr P. Vorster of the National Herbarium, the staff of the Botany Department and Mr P. Hasse of the Latin Department, University of Pretoria, for their generous help and advice.

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A NEW PUTATIVE INTER-GENERIC STAPELIAD HYBRID (ASCLEPIADACEAE)

P. V. BRUYNS

ABSTRACT

A putative *Duvalia-Piaranthus* hybrid from the Vanrhynsdorp district is described. Reference is made to its probable parentage.

UITTREKSEL.

'N VERMEENDE INTER-GENERIESE STAPELIA-KRUISING (ASCLEPIADACEAE) 'n Vermeende *Duvalia-Piaranthus* kruising van die Vanrhynsdorp distrik is beskryf met verwysing na die moontlike afkoms daarvan.

Introduction

Natural hybridization between the genera of the Stapelieae is a little recorded phenomenon. Two species, *Hoodiopsis triebneri* Luckhoff and *Luckhoffia beukmanii* Wh. et Sl. are mentioned by White and Sloane (1937) as being of possible natural hybrid origin. This paucity of such hybrids is surprising as it is often found that three or more species of Stapelieae, not necessarily of the same genus, occur within a relatively small area. This may be caused by slightly differing coronal and staminal-column structures preventing pollinia of one plant from effecting pollination on any other, not of its own genus.

X Duvaliaranthus albostriatus Bruyns hybrida nova, hybrida inter Duvalia radiata Haw. et Piaranthus sp.

Planta succulenta, glabra; caulibus decumbentibus, 5–9 cm longis, usque ad 2,5 cm crassis, tetra- vel pentagonis, tuberculatis, glabris, viridibus; floribus aggregatis 2–5, productis inter angulos ex parte apicale caulium; pedicellis erectis, usque ad 3 cm longis, glabris, 2 mm diam.; sepalis 4 mm longis, 2 mm latis basi, acutis, glabris; corolla 3–3,5 cm diam., purpureo-brunnea, angustis albis transversis striatis in annulo et prope annulum; tubo 2 mm altitudine, papillato solum circum orem; lobis paulo reflexis, 1,2–1,4 cm longis, 4 mm latis basi, ¾ lobis replicatis; annulo paulo elevato, obscuro pentagono, paucis minutis papillis, 5–7,5 mm diam.; corona lobis exterioribus rubro-brunneis, apicibus rotundatis; lobis interioribus 1,5 mm longis, rubro-brunneis, super antheras incumbentibus; staminale columna staminibus 5, affixis basi corollae, conjunctis in tubum circum ovarem, adnatis ad complanatum apicem styli; antheris sine terminalibus appendicibus, inflexis in apice styli; polliniis solitariis in unaquisque antherae cellula, horizonta-

libus, pellucidis in interiore margine apud apicem, affixis per latas planas caudiculas lateralibus expansionibus pollinis geronis; *pollinis geronibus* parvis, brunneis.



FIG. 1. Duvaliaranthus albostriatus, face view of flower X2 (approx.)

Type Material: CAPE—3118 (Vanrhynsdorp): Farm Vierfontein, 17 miles north-east of Vanrhynsdorp on road to Nieuwoudtville (-BD), Bruyns 91/75 (NBG, holotype).

DESCRIPTION

Stems: decumbent, 5 to 9 cm long, up to 2,5 cm thick, glabrous, dull green, 4–5 angled, angles irregularly arranged, tuberculate.

Flowers: in groups of 2–5, arising between the angles, near the tip of the stem, developing successively.

Pedicels: erect, up to 3 cm long, glabrous, 2 mm in diameter.

Sepals: 4 mm long, 2 mm wide at base, acute, glabrous.

Corolla: 3 to 3,5 cm in diameter, dull purple-brown with narrow, transverse, white bands on and around the annulus, surface not rugose, lobes glabrous, slightly reflexed (by about 30 deg.), 1,2 to 1,4 cm long, 4 mm broad at the base, replicate for three-quarters of length, tube 2 mm in depth, papillate only around mouth. Annulus slightly raised above corolla surface, obscurely pentagonal, with a few minute papillae, 5 to 7,5 mm in diameter.

Outer corona: 5-lobed, reddish-brown, only very slightly raised above annulus, apices of lobes rounded, sinuses between the lobes concave.

Inner corona: lobes 1,5 mm long, with a dorsal projection about 0,7 mm from tip, reddish-brown, incumbent on anthers.

Staminal column: stamens 5, attached at base of corolla, united into a tube around the ovary, adnate to flattened top of style, anthers without terminal appendages, inflexed on the top of the style. Pollen masses solitary in each anther cell, horizontal, pellucid on inner margin near apex, attached by broad, flat caudicles to lateral expansions of the pollen carrier (these expansions are about half as long as pollen mass), pollen carrier small, brown.

DISCUSSION

A single plant was found near the foot of Vanrhyn's Pass in alluvial soil among *Duvalia radiata* Haw. and a *Piaranthus* sp. Other Stapelieae collected in the area were: *Echidnopsis framesii* Wh. et Sl., *Pectinaria saxatilis* N.E.Br. and *Caralluma mammillaris* N.E.Br none of which bear any significant parental relationship to the hybrid.

The only *Piaranthus* spp. recorded from the Vanrhynsdorp district (White and Sloane, 1937) are *P. punctatus* R.Br. and *P. framesii* Pillans. The involvement of one of these species in the cross would explain the striation on the corolla of the hybrid. The stems are typically tuberculate as in *Duvalia radiata* Haw. and indeed can only be distinguished from those of this species by their elongation and the irregular arrangement of tubercles.

It differs from *D. radiata* however in the erect habit of the pedical, the very inconspicuous annulus and the 5-lobed outer corona. The inner corona differs from that of *D. radiata* in colour and in that the dorsal projection on each lobe in *D. radiata* is considerably broader at the base than at any part of the rest of the lobe, while in the hybrid it is the same width as the remainder of the lobe.

As the genus *Piaranthus* lacks an outer corona this accounts for the reduction of the typical obscurely pentagonal, entire outer corona of *Duvalia radiata* to a series of 5 distinct lobes in the hybrid.

CONCLUSION

In the light of the above the hybrid is concluded to be a cross between *Duvalia radiata* Haw. and a *Piaranthus* sp. The name **X Duvaliaranthus albostriatus** is proposed.

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STUDIES IN CYPERACEAE IN SOUTHERN AFRICA: 8. TWO NEW SPECIES OF CYPERUS L.

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ABSTRACT

Two new species of Cyperus L. are described for Southern Africa.

Jittreksel

STUDIES VAN CYPERACEAE IN SUIDELIKE AFRIKA: 8. TWEE NUWE SOORTE $\it{CYPERUS}$ L.

Twee nuwe soorte van Cyperus L. word beskryf.

During the course of a study of *C. prolifer* Lam. two new taxa were recognized in the genus *Cyperus* L. On the basis of inflorescence shape and the leafless culms, they are assigned to the section *Textiles* of the subgenus *Pycnostachys* (Clarke, 1901).

Cyperus sensilis Baijnath, species nova C. *prolifer* Lam. affinis, a quo imprimis differ alabastris minoribus anguste ovoideis, radiorum receptaculis filiformibus et radiis brevioribus angulum actum cum receptaculo efformantibus.

Perennis, erectus, 40,0–99,0 cm altus, grosse caespitosus: rhizoma horizontale, lignosum; internodia 0,9– $2,6 \times 0,3$ –0,6 cm, vaginis persistentibus multinerviis griseo-brunneis vestita: folia ad vaginas radact; vaginae 7,4– $28,5 \times 0,3$ –2,5 cm, glabrae, multinerviae; laminae deficientes: culmi teretes, glabri: inflorescentia alabastra anguste ovidea, 1,6 cm longa: bracteae involucrales 3,1–2 steriles, inflorescentiam haud excedentes: inflorescentia 3,8– $8,2 \times 2,8$ –7,4 cm; radii 25–57, racemosi, 5,6 cm longi, angulum acutum cum apice culmi efformantes, prophyllis tubulosis vaginati, 0,5 cm longi; radii capillares frequentes; radiorum receptaculum elongatum, filiforme: spiculae in quodam radio 24–123, 5,0– $8,0 \times 0,5$ –1,5 mm, planae, ellipticae vel anguste ovatae, flavo—virentes vel ochraceae; rhachilla recta, pallide flava: glumae infimae 1–3 steriles, ceterae fertiles, 1,5– $2,0 \times 0,4$ –0,6 mm, anguste ovatae, glabrae, pallide flavae, trinerves, nervo medio in mucronem minutum excurrente: stamina 3; antherae $1,0 \times 0,3$ mm: flavae, cristatae: filamentum antherae aequilongum; pallide flavum: stylus 0,8 mm longus, ochraceus; styli ramuli 3,2–4 mm longi, fusco-brunnei, papillosi: achaenium

Accepted for publication 28th July, 1976.

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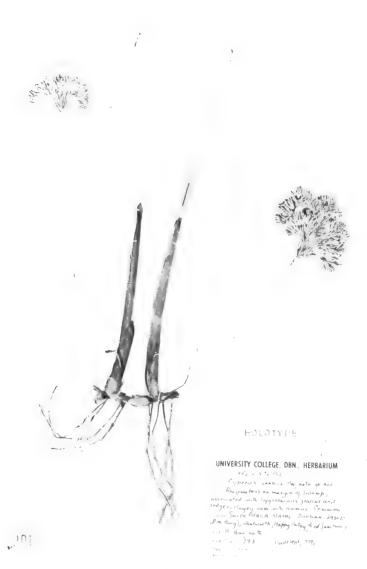


Fig. 1. The holotype of *Cyperus sensilis* Baijnath.

maturum, 0.6×0.4 mm, obovatum stipitatum; cellulae extimae rectangulares marginibus sinuosis.

Type: NATAL—2930 (Pietermaritzburg): Durban Wentworth, Happy Valley Bird Sanctuary, September, 1970 (-DD), Baijnath 793 (IU, holotype; K, NU, MO, P, PRE).

Perennial, erect, 40-99 cm high in large clumps: rhizome horizontal, frequently vertical, ligneous; internodes $0.9-2.6 \times 0.3-0.6$ cm, clothed by many-nerved. grey-brown, persistent sheaths: leaves limited to sheaths; sheaths 7,4-28,5 × 0,3-2,5 cm, glabrous, many-nerved, nerves converging at apex, margin of mouth scarious; blades generally absent: culms terete, glabrous: inflorescence-bud, narrowly ovoid, up to 1,6 cm long: involucral bracts generally 3, 1-2 barren, not exceeding inflorescence: inflorescence 3,8-8,2 × 2,8-7,4 cm; rays 25-57, racemose, up to 5,6 cm long, forming acute angle with culm apex, sheathed at base by tubular prophylls, 0,5 cm long; capillary rays common; ray receptacle elongated, filiform: spikelets 24-123 on each ray, 5-8 × 1,5 mm, generally elliptic or narrowly ovate, yellow green or yellow brown, darkening on drying and age; rhachilla straight, pale vellow; glumes lowermost 1-3 sterile, remainder fertile, $1,5-2,0 \times 0,4-0,6$ mm, narrowly ovate, base truncate, glabrous, pale yellow, margin scarious, keel three-nerved, central nerve excurrent into minute mucron: stamens 3; anthers 1.0×0.3 mm, yellow, crested; filament as long as anther, pale yellow: style 0,8 mm long, yellow brown; style branches 3, 2,4 mm long, black brown, papillate: achene when mature, 0,6 × 0,4 mm, obovate, with concave sides, stipitate; outermost cells rectangular, with markedly sinuous margins.

Flowering period September to February inclusive.

SPECIMENS EXAMINED

NATAL—2832 (Mtubatuba): Makhakhatana, -11/1969 (-AB), *Ward 6804* (IU); Hlabisa, W. of Charter's Creek, -/11/1955, *Ward 2781* (K, NH, NU, NPB).

—2930 (Pietermaritzburg): Wentworth Happy Valley Bird Sanctuary, –/9/1970 (-DD), *Baijnath* 793 (IU, K, MO, NU, P, PRE); Merebank, Clairwood Race, Course, –/12/1969, *Baijnath* 666, 669 (IU).

—3030 (Port Shepstone): Umdoni Park, -/2/1970 (-BC), Baijnath 733 (IU).

C. sensilis was first collected in 1955 (Ward 2781) in a seasonal pan west of Charter's Creek and has subsequently been collected from similar habitats further north (Ward 6804) and as far south as Umdoni Park.

The original specimen was tentatively identified as *C. prolifer* Lam. on the basis of Clarke's (1901) key, but as has been pointed out in a previous paper (Getliffe and Baijnath, 1976) the criterion on which Clarke distinguished his taxon is invalid.

C. sensilis is always associated with seasonal pans where it forms a conspicuous zone near the water's edge. It may be recognized by its dark glossy terete culms and narrow umbellate inflorescence borne on an elongate receptacle. Unlike C.

prolifer (C. isocladus Kunth) the umbel rays do not expand unless conditions are favourable and populations either exhibit dormant buds or fertile expanded inflorescences. This species has never been seen to expand sterile rays.

Vegetative proliferation in this species appears to be restricted to the production of slender grass-like culm growth from the rhizomes.

C. sensilis, so named to indicate its sensitivity to flowering conditions, is believed to be closely related to C. x turbatus and may be one of the parents of this putative hybrid.

Cyperus x turbatus Baijnath, sp. nov., inter *C. proliferum* Lam. et *C. sensilem* Baijnath quasi intermedius, verosimiliter ex origine hybrida inter has species exhortus; ab utraque forma inflorescentiae aliena et receptaculo radiorum ovoideo cum extensionibus, a *C. prolifero* insuper radiis paucioribus et a *C. sensili* bracteis involucralibus longioribus recedit.

Perennis, erectus vel cernuus 29,0–108,0 cm altus, grosse caespitosus: rhizoma horizontale, lignosum; internodia 0,7-3,2 × 0,3-0,6 cm, persistentibus fuscis multinerviis vestita: folia ad vaginas redacta; vaginae $6.5-24.5 \times 0.3-2.5$ cm, glabrae, multinerviae; laminae deficientes; culmi triquetri vel teretes, plerumque trigoni, glabri: inflorescentia alabastra late ovoideum vel ellipticum, 2,5 cm longum: bracteae involucrales 3-5, quarum 1-2 steriles, inflorescentiam haud excedentes: inflorescentia $4.5-15.0 \times 4.0-12.6$ cm; radii 42-73, racemosi, 8.3 cm longi, angulum obtusum cum apice culmi efformantes, prophyllis tubulosis 0,8 cm longis vaginati; radii capillares frequentes; radiorum receptaculum ovoideum, cum extensionibus filiformibus 1–2: spiculae in quoque radio 12–75, $5,0-13,0 \times$ 0,5-1,5 mm, planae ellipticae vel anguste ovatae, flavo-virentes vel ochraceae; rhachilla recta, pallide flava: glumae 1-3 infimae steriles, ceterae fertiles, 1,4-1,9 × 0.3–0.5 mm, late ovatae, glabrae, cremeae, trinerves, nervo medio in mucronem minutum excurrente: stamina 3; antherae 0,9 × 0,2 mm, ochraceae, cristate; filamentum antherae aequilongum, flavum; stylus 0,7 mm longus, ochraceus; styli ramuli 3, 0,9 mm, longi fusco -brunnei, papillosi: achaenium maturum 0,5 × 0,2 mm, obovatum, stipitatum; cellulae extimae quadratae, marginibus sinuosis.

Type: NATAL—3030 (Port Shepstone): Park Rynie, off Main South Coast Road (-BC), December 1970, *Baijnath 824* (NBG, holo; K, NU, IU, holotype; K, NU, MO, P, PRE).

Perennial, erect or nodding, 29–108 cm high, in large clumps: rhizome horizontal, frequently vertical ligneous; internodes, $0,7-3,2 \times 0,3-0,6$ cm clothed by many-nerved, blackish, persistent sheaths: leaves limited to sheaths; sheaths $6,5-24,5 \times 0,3-2,5$ cm, glabrous, many-nerved, nerves converging at apex, margin of mouth scarious; blades generally absent: culms triquetrous or terete, generally trigonous, glabrous: inflorescence-bud broadly ovoid to elliptic up to 2,5 cm long: $involucral\ bracts$ 3–5 in number, 1–2 barren, not exceeding inflorescence: inflorescence 4,5–15 \times 4–12,6 cm; rays 42–73 in number, racemose up to



Fig. 2.

The holotype of *Cyperus x turbatus* Baijnath, a putative hybrid associated with seasonal pans along the coast of Natal.

8,3 cm long, forming obtuse angle with culm apex, sheathed at base by tubular prophylls, 0,8 cm long; capillary rays common; ray receptacle ovoid, with 1–2 filiform projections: spikelets, 12–75 on each ray, 5–13 \times 0,5–1,5 mm, generally flat, elliptic or narrowly ovate, yellow green or yellow brown, darkening on drying and age; rhachilla straight, pale yellow: glumes lowermost 1–3 sterile, remainder fertile, 1,4–1,9 \times 0,3–0,5 mm; broadly ovate, base truncate, glabrous, cream, margin scarious, keel three-nerved, central nerve excurrent into minute mucron: stamens 3; anthers 0,9 \times 0,2 mm, yellow brown, crested; filament as long as anther, yellow with small brown markings: style 0,7 mm long, yellow brown; style branches 3, 0,9 mm long, black brown, papillate: achene mature 0,5 \times 0,2 mm, obovate with concave sides, stipitate; outermost cells quadrate, with markedly sinuous margins.

Flowering period November to February inclusive.

SPECIMENS EXAMINED

NATAL—2832 (Mtubatuba): Mpati, -/11/1969 (-AD), Baijnath 661 (IU).

—2930 (Pietermaritzburg): Merebank, Clairwood Race Course, -/12/1969 (-DD), Baijnath 668, 670 (IU).

—3030 (Port Shepstone): road to Park Rynie -/1/1967 (-BC), *Strey* 7290 (IU, K, NU, PRE); Park Rynie -/12/1970, *Baijnath* 824 (IU, K, MO, NU, P, PRE); Umdoni Park, -/2/1970, *Baijnath* 822 (IU); Shelley Beach, -/5/1970 (-CD), *Baijnath* 814, 815, 816 (IU).

C. x turbatus is closely associated with disturbed damp habitats where drainage is impeded by road construction or excessive trampling. It is less tolerant of stagnant conditions than C. sensilis and under prolonged stagnant conditions exhibits vegetative proliferation by means of activity of latent buds in axils of the larger inflorescence bracts.

In inflorescence form it is intermediate between the spherical umbel of *C. prolifer* Lam. and narrow obconical umbel of *C. sensilis* but like the former, has been seen with both sterile and fertile rays.

C. x turbatus was first collected in 1967 (Strey 7290) when it was incorrectly determined as C. denudatus. It has subsequently been found in disturbed habitats on the coast of Natal from Mpati to Shelly Beach. Its morphological resemblance to C. prolifer and C. sensilis suggests close affinity with these two species and it is suggested that it may be of hybrid origin. The taxon does, however, appear to be stable and is readily distinguished from its relatives and is therefore described here as a species although possibility of hybrid origin has not been excluded.

HERBARIUM ABBREVIATIONS

The Herbarium abbreviations are those listed by Holmgren, P. K. and Keuken, W. (1974). In addition, the following abbreviation is included:

IU—Herbarium of the University of Durban–Westville.

ACKNOWLEDGEMENTS

The author acknowledges, with gratitude, the financial assistance of the South African Council for Scientific and Industrial Research, the South African Sugar Association and the S.C.D.I.F.A. and Maistry Educational Trusts who provided a travel grant to Mauritius. Grateful appreciation is extended to the Directors of Herbaria for loan of material; to Mr H. K. Airy Shaw for undertaking the Latin descriptions and to Mr Ganga for his valuable assistance. The Author thanks Prof. O. A. M._Lewis and Prof. T. D. Steinke of the Botany Department of the University of Durban–Westville, and their staff, including his supervisor Dr F. M. Getliffe, for their guidance and encouragement, and is grateful to Dr K. D. Gordon-Gray for her helpful comments on the preparation of the manuscript.

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FRESHWATER ALGAE OF SOUTHERN AFRICA: 3. PLEUROTAENIUM BREVE RACIBORSKI VAR. ENGLERI (SCHMIDLE) KRIEGER AND PENIUM GONATOZYGIFORME CLAASSEN SP. NOV. FROM TRANSVAAL

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ABSTRACT

Pleurotaenium breve Raciborski var. engleri (Schmidle) Krieger is reported for the first time from South Africa and a new desmid species, Penium gonatozygiforme Claassen, is described.

UITTREKSEL

VARSWATERALGE VAN SUIDELIKE AFRIKA: 3. PLEUROTAENIUM BREVE RACIBORSKI VAR. ENGLERI (SCHMIDLE) KRIEGER AND PENIUM GONATOZYGIFORME CLAASSEN SP. NOV. VAN TRANSVAAL

Pleurotaenium breve Raciborski var. engleri (Schmidle) Krieger is vir die eerste keer in Suid-Afrika aangetref. 'n Nuwe Penium-spesie word beskryf naamlik Penium gonatozygiforme Claassen.

MATERIAL AND METHODS

Samples containing *Pleurotaenium breve* var. *engleri* and *Penium gonatozygi-forme* were collected from a small pan 16 km east of Ottosdal in the Southwestern Transvaal (approximately 26° 48′ S and 26° 07′ E). This particular pan originated from a pit from which gravel had been collected for road constructions several years previously.

The samples consisted of reddish-brown sediments collected in shallow stagnant water 5–75 mm deep. Two samples were collected on 4th April, 1972, and eight on 12th February, 1975. During December 1974 the pan was completely dry.

The hydrogen-ion concentration and the temperature of the water at the time of collection were pH 7,7 and 24°C, and pH 7,5 and 27°C for April 1972 and February 1975 respectively.

The material was preserved in 4% formalin.

Slides were made by mounting a sample droplet in a drop of glycerine.

Drawings were made with a Zeiss binocular bright field/phase contrast microscope using a Leitz micrometer-net-ocular and specially printed squared paper, the squares being 2 \times 2 cm. The lenses used were a 12,5 \times eye-piece and a 40 \times objective.

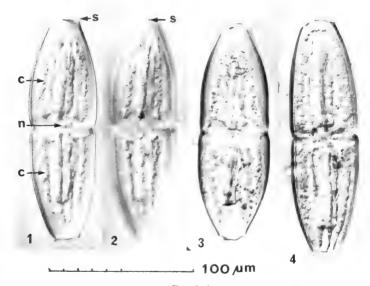
Photomicrographs were taken on Adox KB14 film using a 35 mm Willd microscope camera on a Zeiss Nomarski contrast microscope. A 6 \times eye-piece and a 40 \times objective were used.

All dimensions are given in micrometres (μ m).

OBSERVATIONS AND DISCUSSION

Pleurotaenium breve Raciborski var. engleri (Schmidle) Krieger. (Figs 1–7).

This desmid was originally described by Schmidle (1898, p. 23) as *Pleurotaenium engleri* from material collected in Central East Africa during June 1892. He mentioned that the taxon could be compared with *Pleurotaenium breve* Raciborski. Krieger (1937, p. 410) gave the taxon varietal rank under Raciborski's species. From the dimensions given by Schmidle (length 120, width 36) it is assumed that he found only one specimen.

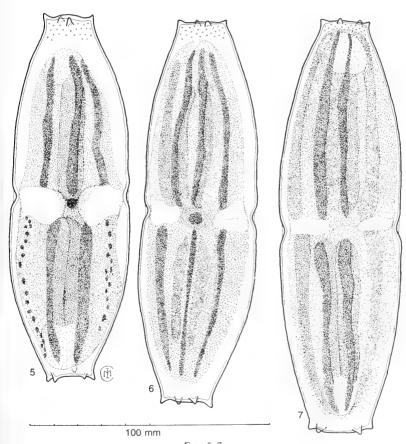


Figs 1-4.

Photomicrographs of *Pleurotaenium breve* var. *engleri*. Figs 1, 3, 4. Morphology of the cell and chloroplasts. Fig. 2. The same specimen as in Fig. 1, showing the ridges of the chloroplasts. c, chloroplast; n, nucleus; s, spine.

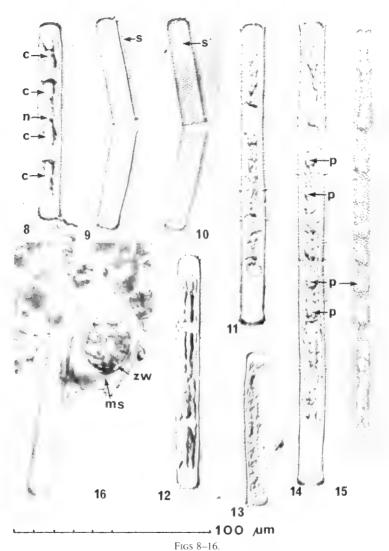
No further mention was made of this taxon in literature available to the present author until Lind (1971, p. 538) rediscovered it in material collected in Uganda during 1967. From the dimensions given by Lind (length 105, width 36) it is assumed that she, too, found only one specimen.

Since the present author examined more than a hundred slides and found only three specimens in the material collected in 1972 and none in the material collected in 1975, it is evident that this taxon is extremely rare. Although these specimens are larger than those found by Schmidle and Lind they are still regarded as members of the same taxon and not as a new form. The dimensions of the specimens are: length 151,8–169,5; maximum width 46,7–50,8; width of isthmus 44–48; width of apices 19,4–25.



Figs 5-7.

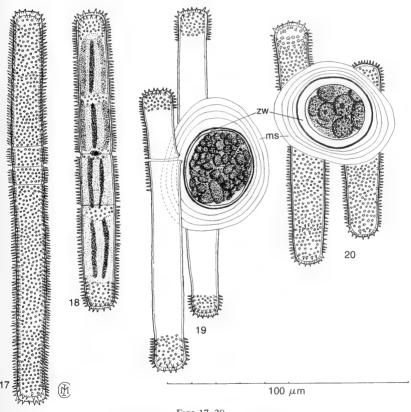
Drawings of *Pleurotaenium breve* var. *engleri* showing the morphology of the cell and chloroplasts.



Photomicrographs of *Penium gonatozygiforme*. Figs 8, 9, 11–14. Various specimens showing the morphology of the cell and chloroplasts. Figs 10, 15. Surface views of Figs 9 and 14 showing the spines. Fig. 16. Conjugating cells with zygospore. c, chloroplast; ms, mucous sheath; n, nucleus; p, pyrenoid; s, spines; zw, zygospore wall.

None of the previous authors made any mention of the chloroplasts of this taxon nor were any depicted in their drawings. In the Ottosdal specimens each semicell contains one axial chloroplast with about 4–6 longitudinal ridges. No pyrenoids were observed.

Schmidle's specimen has four teeth at the apex of each semicell but Lind could distinguish only two. The Ottosdal specimens agree with that of Schmidle except for one specimen which has a fifth, slightly subapical, tooth in one semicell (Fig. 5, bottom semicell).



Figs 17–20.

Drawings of *Penium gonatozygiforme*. Figs 17, 18. Morphology of the cell and chloroplasts. Figs 19, 20. Conjugating cells with zygospores.

ms, mucous sheath; zw, zygospore wall.

Penium gonatozygiforme sp. nov. (Figs 8-20).

Cellulae circiter 5–13,6–plo longiores quam latiores, cylindricae in medio leviter constrictae, apices truncate rotundati. Cellulae paries incolor plurimis munitus spinis acutis late dispersis ac simillimis earum quae in *Gonatozygo aculeato* Hastings inveniuntur. Chloroplasti axiales, bini in semicellulis singulis, at singuli pyrenoidibus singulis vel ternis muniti. Zygospora subglobosa ac levis, vagina lamellata ac mucosa saepta.

Longitudo sine spinis 80–237; cum spinis 81,5–240; latitudo sine spinis 12,4–13,3; cum spinis 16,8–17,6; apicis latitudo sine spinis 10,6–12,4; cum spinis 14–15; zygospora $28 \times 32-33,5$; vagina $36-42 \times 46-52$.

Habit.: Transvaal—2626 (Klerksdorp): in palude parva XVI milia passuum ad orientem ab Ottosdal (—CC).

Holotypus: fig. nostra 17.

Cells about 5–13,6 times longer than their diameter, cylindrical, with a slight median constriction, apices truncately rounded. Cell wall colourless and furnished with numerous scattered acute spines. Chloroplasts axial, two in each semicell, with 1–3 pyrenoids each. Zygospore subglobose and smooth, surrounded by a lamellated mucous sheath.

Length without spines 80–237; with spines 81,5–240; width without spines 12,4–13,3; with spines 16,8–17,6; width of apices without spines 10,6–12,4; with spines 14–15; zygospore $28 \times 32-33,5$; sheath $36-42 \times 46-52$.

Type locality: Transvaal—2626 (Klerksdorp): small pan 16 km E. of Ottosdal (-CC). Holotype: Fig. 17.

This taxon does not correspond to any other *Penium* species in literature available to the author but has a superficial resemblance to *Gonatozygon aculeatum* Hastings (Förster, 1974, Pl. 1, Figs 2–12). It is however distinguished from the latter by the placoderm nature of the cell wall and the two chloroplasts contained in each semicell.

Penium gonatozygiforme was fairly abundant in the samples collected during April 1972 but rather scarce in those collected during February 1975.

ACKNOWLEDGEMENTS

I am indebted to the Council for Scientific and Industrial Research and the Research Committee of the University of Pretoria for financial assistance and to Prof Dr H. L. Gonin who kindly translated the Latin diagnosis.

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A PROVISIONAL CHECK-LIST OF THE ORCHIDACEAE OF ANGOLA

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ABSTRACT

A provisional check-list of 160 species of Orchidaceae in 37 genera recorded from Angola is given, together with relevant synonyms and distribution data.

UITTREKSEL

'N VOORLOPIGE LYS VAN DIE ORCHIDACEAE VAN ANGOLA

'n Voorlopige lys van 160 Orchidaceae soorte ingedeel in 37 genera aangeteken in Angola, tesame met die toepaslike sinonieme en verspreidings data word gemeld.

During the course of preparing the volume on the Pteridophyta for the Conspectus Florae Angolensis in the herbaria of the British Museum (Natural History), London, and the Royal Botanic Gardens, Kew, the opportunity was taken to prepare a provisional check-list of the orchids of Angola as a basis for a possible future contribution to the Conspectus.

The known distribution of each species in Angola, including Cabinda, is indicated according to the districts used in the Conspectus but these have been abbreviated as follows: Cabinda (Cab.), Zaïre (Zaï.), Congo (Con.), Luanda (Lua.), Cuanza Norte (Cu.N.), Cuanza Sul (Cu.S.), Malange (Mal.), Lunda (Lun.), Benguela (Beng.), Bie (Bie), Moxico (Mox.), Cubango (Cub.), Moçamedes (Moc.), Huila (Huil.)

The author is indebted to the Directors of the British Museum (Nat. Hist.) and the Royal Botanic Gardens, Kew, for facilities for work and also to his colleague, Dr A. V. Hall for discussion regarding the genera *Eulophia* and *Satyrium*.

The species are listed in alphabetical order within genera or within currently recognized subgeneric groupings.

Holothrix Rich. ex Lindl. longiflora Rolfe (syn. <i>H. medusa</i> Kraenzl.)	(Huil.)
Schwartzkopffia Kraenzl.	
lastii (Rolfe) Schlechter	(Mal.; Beng.)
(syn. S. angolensis Schlechter) pumilio (Lindl.) Reichb.f.	(Mal.)
Brachycorythis Lindl.	
rhodostachys (Schlechter) Summerh.	(Cub.)
friesii (Schlechter) Summerh.	(Beng.; Bie)

Accepted for publication 12th July, 1976.

tenuior Reichb.f.	(Bie; Cub.; Huil.)
(syn. Diplacorchis angolensis Schlechter) angolensis (Schlechter) Schlechter	(Beng.; Bie)
(syn. <i>Platanthera angolensis</i> Schlechter) oligophylla Kraenzl.	(Cub.)
buchananii (Schlechter) Rolfe	(Mox.)
pleistophylla Reichb.f. var. pleistophylla subsp. leopoldii (Kranzl.) Summerh. ovata Lindl. subsp. welwitschii (Reichb.f.) Summerh. pubescens Harv. (syn. Platanthera brachycorythis Schlechter; B. baumii Schlechter)	(Beng.) (Cab.) (Huil.) (Cu.N.; Lun.; Beng.; Cub.)
mixta Summerh.	(Beng.)
Cynorkis Thou.	(20119.)
anacamptoides Kraenzl. (syn. Stenoglottis calcarata Reichb.f.)	(Huil.)
johnsonii Rolfe	(Mox.)
Habenaria Willd.	
chlorotica Reichb.f.	(Huil.)
filicornis Lindl.	(Cu.N.)
(syn. H. spiranthes Reichb.f.)	()
hologlossa Summerh.	(Mox.)
epipactidea Reichb.f.	(Huil.)
(syn. H. hircina Reichb.f.)	
gabonensis Reichb.f. var. psiloceras (Welw.ex. Reichb.f.) Summerh.	(Cu.N.; Mox.)
(syn. <i>H. psiloceras</i> Welw. ex Reichb.f.)	(Cub.)
zambesina Reichb.f. macrandra Lindl.	(Cub.) (Cu,N.)
(syn. <i>Podandria macrandra</i> (Lindl.) Rolfe)	(Cu.N.)
anaphysema Reichb.f.	(Bie; Huil.)
cataphysema Reichb.f.	(Huil.)
compta Summerh.	(Cub.)
genuflexa Rendle	(Cu.N.)
(syn. H. confusa Rolfe)	X =
huillensis Reichb.f.	(Mal.; Beng.; Huil.)
ichneumonea (Sw.) Lindl.	(Beng.; Cub.)
kilimanjari Reichb.f.	(Mox.)
kubangensis Schlechter	(Cub.)
robusta Welw. ex Reichb.f.	(Cu.N.)
strangulans Summerh.	(Huil.)
weberana Schlechter	(Mox.)
welwitschii Reichb.f.	(Beng.; Huil.)
(syn. <i>H. keiliana</i> Kraenzl.) holubii Rolfe	(Mox.; Cub.)
stenorhynchos Schlechter	(Mox.; Cub.)
decaptera Reichb.f.	(Mal.)
macroplectron Schlechter	(Beng.; Mox.; Cub.)
dregeana Lindl.	(Huil.)
(syn. H. calva (Reichb.f.) Rolfe)	\ · · · · · · /
divergens Summerh.	(Mal.)
holothrix Schlechter	(Cub.)
macrura Kraenzl.	(Mal.; Beng.)
(syn. H. pentaglossa Kraenzl.)	

mechowii Reichb.f. verdickii (De Wild.) Schlechter (syn. <i>H. monophylla</i> Schlechter)	(Mal.; Beng.) (Cub.)
Platycoryne Reichb.f. brevirostris Summerh. guingangae (Reichb.f.) Rolfe (syn. <i>Habenaria guingangae</i> Reichb.f.)	(Mox.) (Cu.N.; Lun.)
heterophylla Summerh. micrantha Summerh. protearum (Reichb.f.) Rolfe	(Cub.) (Lun.; Mox.) (Cub.; Huil.)
(syn. Habenaria protearum Reichb.f.) trilobata Summerh.	(Beng.)
Centrostigma Schlechter occultans (Welw. ex Reichb.f.) Schlechter papillosum Summerh.	(Huil.) (Beng.)
Disa Berg. celata Summerh. erubescens Rendle	(Beng.) (Mox.)
ochrostachya Reichb.f. welwitschii Reichb.f. compta Summerh.	(Bie; Huil.) (Bie; Cub.; Huil.) (Beng.; Bie)
hircicornis Reichb.f. versicolor Reichb.f. equestris Reichb.f.	(Bie; Cub.) (Huil.) (Beng.; Bie; Cub.; Huil.)
(syn. <i>D. huillensis</i> Fritsch) similis Summerh.	(Beng.)
Satyrium Sw. ivantalae Reichb.f. longicauda Lindl. var. buchanani (Schlechter) Hall riparium Reichb.f. leucocomos Reichb.f.	(Huil.) (Beng.) (Beng.; Huil.) (Beng.; Huil.)
(syn. S. longibracteatum Rolfe) mechowianum Kraenzl. oliganthum Schlechter	(Mal.) (Cub.)
trinerve Lindl. (syn. S. atherstonei Reichb.f.; S. proschii Briq.) welwitschii Reichb.f. (syn. S. mechowii Reichb.f.; S. paludosum Reichb.f.)	(Bie; Cub.) (Mal.; Beng.; Bie; Huil.)
Disperis Sw. aphylla Kraenzl. ex De Wild & Dur. katangensis Summerh. reichenbachiana Welw. ex Reichb.f. thomensis Summerh.	(Cu.N.) (Mox.) (Cu.N.; Mox.) (Mox.)
Vanilla Mill. imperialis Kraenzl. polylepis Summerh.	(Lua.; Mox.) (Mox.)
Nervilia Comm. ex Gaudich. shirensis (Rolfe) Schlechter umbrosa (Reichb.f.) Schlechter viridiflava (Reichb.f.) Schlechter	(Beng.) (Cu.N.) (Mal.)
Epipogium Gmel. roseum Lindl. (syn. E. nutans Reichb.f.)	

Platylepis A. Rich. glandulosa (Lindl.) Reichb.f.	(Cab.; Cu.N.)
(syn. Diplogaster angolensis Reichb.f.)	
Zeuxine Lindl. africana Reichb.f.	(Cu.N.)
Corymborkis Thou.	
corymbosa Thou. (syn. Corymbis welwitschii Reichb.f.)	(Cu.N.)
Liparis Rich.	
guingangae Reichb.f.	(Huil.)
nervosa (Thunb.) Lindl.	(Mox.; Cub.)
welwitschii Reichb.f.	(Cu.N.)
	(Cu.14.)
Ansellia Lindl.	a Gi na
africana Lindl. var. australis Summerh.	(Lua.; Cub.; Huil.)
Polystachya Hook.	
albescens subsp. imbricata (Rolfe) Summerh.	(Cu.N.)
adansoniae Reichb.f.	(Cu.N.)
angularis Reichb.f.	(Cu.N.)
golungensis Reichb.f.	(Cu.N.)
modesta Reichb.f.	(Cu.N.)
mukandaensis De Wild.	(Cu.N.)
(syn. <i>P. huvghei</i> De Wild.; <i>P. plehniana</i> Schlechter).	(Cu.1v.)
nitidula Reichb.f.	(Cu.N.)
odorata Lindl.	(Lun.)
tessellata Lindl.	(Mox.; Cub.)
(syn. P. buchananii Rolfe)	(T)
affinis Lindl.	(Lun.)
tayloriana Rendle	(Cong.; Lun.; Cub.)
(syn. P. holochila Schlechter)	
Calanthe R.Br.	
corymbosa Lindl.	(Mox.)
Phaius	(,
1 1141110	(Cub.)
occidentalis Schlechter	(Cub.)
Bulbophyllum Thou.	
cocoinum Lindl.	(Cu.N.)
(syn. B. andongense Reichb.f.)	
distans Lindl.	(Beng.)
intertextum Lindl.	(Lun.)
oreonastes Lindl.	(Lun.)
platyrachis Rolfe	(Mal.)
rupincola Reichb.f.	(Cu.N.)
•	(Ca.11.)
Eulophidium Pfitz.	
maculatum (Lindl.) Pfitz.	(Cu.N.)
(syn. E. ledienii Stein)	
Eulophia R.Br. ex Lindl.	
aloifolia Reichb.f.	(Cu.N.)
	(Mal.; Lun.; Cub.; Huil.)
angolensis (Reichb.f.) Summerh.	(Mai., Luii., Cub., Huii.)
(syn. E. antunesii Rolfe; Lissochilus platypertus	
Reichb.f.)	(Mal.)
antennisepala (Reichb.f.) Schlechter	(Mal.)
arenicola Schlechter	(Cub.)
baumiana Kraenzl.	(Cub.)

bouliawongo (Reichb.f.) Raynal	(? Cab.)
(syn. Lissochilus giganteus Welw. ex Reichb.f.;	
L. elatus Rolfe)	
calantha Schlechter	(Beng.; Cub.)
var. kubangensis Schlechter	(Cub.)
chrysops Summerh.	(Cu.N.)
(syn. Lissochilus aurantiacus Rechb.f.)	
coeloglossa Schlechter	(Cub.)
cucullata (Sw.) Steud.	(? Cab.; Cong.; Cu.S.; Mal.;
(syn. E. dilecta (Reichb.f.) Schlechter;	Beng.; Mox.; Cub.)
E. monteiroi Rolfe)	beng., Mox., eub.)
dictyostegioides Kraenzl.	(Cub.)
euglossa (Reichb.f.) Reichb.f.	(Cu.N.)
fridericii (Reichb.f.) Hall	(Cu.N.)
gracilis Lindl.	(Lun.)
guineensis Lindl.	(Lua.; Cu.N.)
horsfallii (Batem.) Summerh.	(Mal.; Beng.; Huil.)
(syn. Lissochilus welwitschii Reichb.f.);	(Mai., Beng., Hun.)
L. alexandri Reichb.f.)	
ischna Summerh.	(Mox.; Cub.)
(syn. E. macra Schlechter non Ridl.)	(Mox., Cub.)
latilabris Summerh.	(May)
	(Mox.)
livingstoniana (Reichb.f.) Schlechter	(Mal.; Bie; Cub.)
(syn. Lissochilus malangensis Reichb.f.)	(C. N.)
longifolia (HBK) Schlechter	(Cu.N.)
(syn. E. woodfordii Rolfe)	(D.)
longisepala Rendle	(Beng.)
malangana (Reichb.f.) Summerh.	(Mal.; Mox.; Cub.)
(syn. E. warburgii Schlechter; E. rigidifolia	
Kraenzl.)	(2 # 3 ·
mechowii (Reichb.f.) Dur. & Schinz	(Mal.)
monile Reichb.f.	(Huil.)
nuttii Rolfe	(Cub.)
(syn. E. corymbosa Schlechter)	
odontoglossa Reichb.f.	(Cu. S.; Beng.)
(syn. E. shupangae (Reichb.f.) Kraenzl.)	_
protearum Reichb.f.	(Beng.)
pyrophila (Reichb.f.) Summerh.	(Cab.)
rolfeana Kraenzl.	(Cub.)
rugulosa Summerh.	(Mal.)
(syn. Lissochilus mechowii Reichb.f.)	
speciosa (R.Br. ex Lindl.) Bol.	(Lua.; Cub.)
(syn. Lissochilus volkensii Rolfe)	
streptopetala Lindl.	(Cu.N.; Huil.)
(syn. Lissochilus paiveanus Reichb.f.; ? L. renschianus	
Reichb.f.)	
welwitschii (Reichb.f.) Rolfe	(Mal.; Beng.; Cub.; Huil.)
(syn. Orthochilus welwitschii Reichb.f.;	
O. renschianus Reichb.f.; E. bicolor Reichb.f. &	
Sonder non Blume; E. dichroma Rolfe)	
Calyptrochilum Kraenzl.	
christyanum (Reichb.f.) Summerh.	(Mal.)
(syn. Angraecum malangeanum Kraenzl.;) A. mombasens	e
Rolfe; A. zigzag De Wild. A. bokoyense De Wild.; A	1.
ovatifolium De Wild.; C. orientale Schlechter)	
emaraginatum (Sw.) Schlechter	(Lun.)
	•

Podangis Schlechter	(C., N.)
dactyloceras (Reichb.f.) Schlechter	(Cu.N.)
Angraecum Bory distichum Lindl. eichlerianum Kraenzl.	(Lun.) (Lun.)
Microcoelia Lindl. guyoniana (Reichb.f.) Summerh.	(Cu.N.)
Diaphananthe Schlechter bidens (Sw. ex Pers.) Schlechter fragrantissima (Reichb.f.) Schlechter rutila (Reichb.f.) Summerh. (syn. Angraecum woodianum Schlechter) welwitschii (Reichb.f.) Schlechter xanthopollinia (Reichb.f.) Summerh. (syn. Aeranthes erythropollinius Reichb.f.)	(Lun.) (Cu.N.) (Cu.N.; Lun.) (Cu.N.) (Cu.N.)
Bolusiella Schlechter iridifolia (Rolfe) Schlechter	(Cu.N.)
Aerangis Reichb.f. calantha (Schlechter) Schlechter flabellifolia Reichb.f.	(Lun.) (Cu.N.)
Rangaeris (Schlechter) Summerh. muscicola (Reichb.f.) Summerh. rhipsalisocia (Reichb.f.) Summerh. (syn. Listrostachys trachypus Kraenzl.)	(Cu.N.) (Cu.N.)
Cyrtorchis Schlechter monteiroae (Reichb.f.) Schlechter	(Cong.)
Solenangis Schlechter clavata (Reichb.f.) Schlechter	(Cab.)
Eurychone Schlechter galeandrae (Reichb.f.) Schlechter	(Cu.N.)
Tridactyle Schlechter tridactylites (Rolfe) Schlechter tridentata (Harv.) Schlechter	(Cu.N.) (Cab.)

A PROVISIONAL CHECK-LIST OF THE ORCHIDACEAE OF MOZAMBIQUE

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ABSTRACT

A provisional check-list of 151 species of Orchidaceae in 41 genera recorded from Mozambique is given, together with relevant synonyms and distribution data. *Eulophia mossambicensis* Schelpe nom. nov. is proposed for *E. humilis* Schlechter *non* Rendle.

UITTREKSEL

'N VOORLOPIGE LYS VAN DIE ORCHIDACEAE VAN MOSAMBIEK

'n Voorlopige lys van 151 Orchidaceae soorte, ingedeel in 41 genera aangeteken in Mosambiek, tesame met die toepaslike sinonieme en verspreiding data word gemeld. Eulophia mossambicensis Schelpe nom. nov. word voorgestel vir E. humilis Schlechter non Rendle.

On two expeditions to Mozambique, one to Gorongosa Mountain and the area along the border with Rhodesia in 1955 and another to northern Mozambique in 1962 (Schelpe, 1965), the author has been able to collect and subsequently grow a number of orchid species from these areas to flowering. Also study of Mozambique orchids at Kew Herbarium has made it possible to produce this provisional check-list. Abbreviations indicating the known distribution areas of individual species in Mozambique are those used in the *Flora Zambesiaca*.

The author wishes to thank the Director, Royal Botanic Gardens, Kew, for facilities and to express his indebtedness to Dr. A. V. Hall for discussion on *Eulophia* and *Satyrium* and to the late Mr. V. S. Summerhayes for a number of identifications. Thanks are also due to Miss R. Grosvenor of the Government Herbarium, Salisbury, Rhodesia, for many additional records.

Holothrix Rich. ex Lindl. nyasae Rolfe	(N)
Neobolusia Schlechter ciliata Summerh.	(MS)
Schwartzkopffia Kraenzl. lastii (Rolfe) Schlechter	(N)
Brachycorythis Lindl. inhambanensis (Schlechter) Schlechter pleistophylla Reichb.f. subsp. pleistophylla pubescens Harv.	(SS) (MS; Z) (N)
Schizochilus Sond. sulphureus Schlechter lepidus Summerh.	(MS) (MS)

Accepted for publication 12th July, 1976.

Stenoglottis Lindl.	
fimbriata Lindl.	(Z; MS)
(syn. S. zambesiaca Rolfe)	
Cynorkis Thou.	
anacamptoides Kraenzl.	(MS)
anisoloba Summerh.	(MS)
buchanani Rolfe	(Z)
hanningtonii Rolfe	(MS)
kirkii Rolfe	(Z)
oblonga Schlechter	(MS)
Habenaria Willd.	
arenaria Lindl.	(LM)
zambesina Reichb.f.	(Z)
macrandra Lindl.	(MS)
malacophylla Reichb.f.	(MS)
tridens Lindl.	(LM)
kilimanjari Reichb.f.	(N)
(syn. H. martialis Reichb.f.)	
nyikana Reichb.f.	(Z)
macrostele Summerh.	(MS)
welwitschii Reichb.f.	(MS)
(syn. H. leptostigma Schlechter)	(NL MC)
harmsiana Schlechter aberrans Schlechter	(N; MS)
hirsutissima Summerh.	(N) (N)
mosambicensis Schlechter	(MS)
stylites subsp. johnsonii (Rolfe) Summerh.	(N; MS)
subsp. rhodesiaca Summerh.	(MS)
trilobulata Schlechter	(MS)
subarmata Reichb.f.	(T)
Bonatea Willd.	(• /
antennifera Rolfe	(SS)
polypodantha (Reichb.f.) Bolus	(LM)
pulchella Summerh.	(SS)
steudneri (Reichb.f.) Dur. & Schinz	(MS)
*	()
Platycoryne Reichb.f. pervillei Rolfe	(N; Z; MS)
•	(14, 2, 1415)
Disa Bergius	(1) ((1))
zombica N.E. Brown	(MS)
leucostachys Kraenzl.	(MS)
welwitschii Reichb.f.	(N)
versicolor Reichb.f.	(MS)
equestris Reichb.f. concinna N.E. Brown	(N; MS) (MS)
rungweensis subsp. rhodesiaca (Summerh.) Summerh.	(MS)
(syn. D. rhodesiaca Summerh.)	(1413)
hamatopetala Rendle	(MS)
•	(1410)
Brownleea Harv. ex Lindl.	(MC)
parviflora Harv.	(MS)
Satyrium Sw.	
johnsonii Rolfe	(N)
cheirophorum Rolfe	(Z; MS)
(syn. S. speciosum Rolfe; syn. S. morrumbalaensis De Wild.)	(MC)
parviflorum Sw.	(MS)

sphaerocarpum Lindl. longicauda Lindl. neglecfum Schlechter volkensii Schlechter chlorocorys Reichb.f. ex Rolfe breve Rolfe	(LM) (MS) (MS) (MS) (MS) (MS)
Disperis Sw. mozambicensis Schlechter	(MS)
Vanilla Mill. roscheri Reichb.f.	(N; MS; LM)
Nervilia Comm. ex Gaudich. umbrosa (Reichb.f.) Schlechter	(Z)
Corymborkis Thou. corymbosa Thou.	(MS; SS)
Oberonia Lindl. disticha (Lam.) Schlechter	(MS)
Malaxis Soland. ex Sw. katochilos (Schlechter) Summerh.	(MS)
Liparis Rich. neglecta Schlechter	(MS)
Ansellia Lindl. gigantea var. nilotica (Bak.) Summerh. (syn. A. humilis Bull.)	(MS; SS)
Polystachya Hook. albescens var. imbricata (Rolfe) Summerh. transvaalensis Schlechter modesta Reichb.f. tessellata Lindl. golungensis Reichb.f. uniflora De Wild. zambesiaca Rolfe campyloglossa Rolfe lindblomii Schlechter fusiformis (Thou.) Lindl. cultriformis (Thou.) Spreng. (syn. P. lujae De Wild.) tayloriana Rendle sp.nov. aff. P. tayloriana Calanthe R.Br.	(N; Z; MS) (MS) (MS) (N; Z; MS) (MS) (?) (Z; MS) (MS) (Z) (N; Z; MS) (N; Z; MS) (N; Z; MS)
natalensis (Reichb.f.) Reichb.f.	(MS)
Bulbophyllum Thou. intertextum Lindl. mahonii Rolfe oreonastes Lindl. (syn. P. melinostachyum Schlechter) oxypterum (Lindl.) Reichb.f. (syn. B. nyassanum Schlechter; syn. B. platyrachis (Rolfe) Sum sandersonii (Oliv.) Reichb.f.	(MS) (MS) (N; MS) (N; Z; MS) merh.) (MS)
Cirrhopetalum Lindl. umbellatum (Forst. F.) Hook.	(N; MS)

Eulophidium Pfitz.	(MC)
mackenii (Rolfe) Schlechter taenioides (Schlechter) Summerh.	(MS) (MS; SS)
(syn. E. dissimilis Dyer)	(1/15, 55)
decarvanum (Perr.) Summerh.	(MS)
Eulophia R.Br. ex Lindl.	(1110)
angolensis (Reichb.f.) Summerh.	(N)
antennata Schlechter	(N; SS; IM)
biloba Schlechter	(MS)
brevisepala (Rendle) Summerh.	(MS)
(syn. Lissochilus rendlei Rolfe)	
callichroma Reichb.f.	(Z)
caloptera (Reichb.f.) Summerh.	(Z)
cucullata (Sw.) Steud.	(N; Z; MS; SS; LM)
ensata Lindl.	(LM)
flavopurpurea (Reichb.f.) Rolfe	(N)
gastrodioides Schlechter	(MS)
grantii (Reichb.f.) Summerh.	(Z)
(syn. Lissochilus shirensis Rendle; syn. L. oatesii Rolfe) hereroensis Schlechter	(LM)
(syn. E. junodiana Kraenzl.)	(LM)
horsfallii (Bateman) Summerh.	(MS)
kirkii Rolfe	(XIS) (Z)
latilabris Summerh.	(N)
livingstoniana (Reichb.f.) Schlechter	(N; Z; MS)
longisepala Rendle	(MS)
milanjiana Rendle	(Z)
milnei Reichb.f.	(MS)
(syn. E. corallorhiziformis Schlechter)	
mossambicensis Schelpe nom.nov.	(MS)
(pro Eulophia humilis Schlechter in Bot. Jahrb. 26: 337	
(1899) non Rendle (1895))	
norlindhii Summerh.	(N; Z)
odontoglossa Reichb.f.	(Z; LM)
(syn. E. shupangae (Reichb.f.) Kraenzl.; syn. E. aurea	
Kraenzl.)	(NI)
orthoplectra (Reichb.f.) Summerh. paradoxa Kraenzl.	(N) (N; MS)
paradoxa Kraenzi. parviflora (Lindl.) Hall	(MS)
petersii (Reichb.f.) Reichb.f.	(N; Z; MS; LM)
speciosa (R.Br. ex Lindl.) Bol.	(N; Z; MS; SS; LM)
(syn. E. wakefieldii (Reichb.f. & S. Moore) Summerh.)	(11, 2, 115, 33, 211)
streptopetala Lindl.	(Z; MS)
(syn. E. paivaeana (Reichb.f.) Summerh.; syn. L.	
morrumbalaensis De Wild.)	
tenella Reichb.f.	(MS)
walleri Kraenzl.	(N)
(syn. E. angustiflora Kraenzl.)	
welwitschii (Reichb.f.) Rolfe	(Z; MS; SS)
(syn. E. zeyheri Hook.f.; syn. E. lujae De Wild.)	
Pteroglossapsis Reichb.f.	
eustachya Reichb.f.	(MS)
Jumellea Schlechter	(1.10)
filicornoides (De Wild.) Schlechter	(Z)
(syn. Mystacidium walleri Rolfe)	()

Calyptrochilum Kraenzl.	
christyanum (Reichb.f.) Summerh.	(MS)
Angraecum Bory anocentrum Schlechter chamaeanthus Schlechter conchiferum Lindl. cultriforme Summerh. sacciferum Lindl. stolzii Schlechter	(MS; SS) (MS) (MS) (MS) (MS) (MS) (MS)
Acampe Lindl. pachyglossa Reichb.f. (syn. A. nyassana Schlechter)	(N; MS)
Microcoelia Lindl.	
conica (Schlechter) Summerh. exilis Lindl. guyoniana (Reichb.f.) Summerh.	(MS) (N; MS) (Z)
Diaphananthe Schlechter fragrantissima (Reichb.f.) Schlechter rutila (Reichb.f.) Summerh.	(MS) (Z; MS)
Aerangis Reichb.f. appendiculata (De Wild.) Schlechter kirkii (Rolfe) Schlechter kotschyana (Reichb.f.) Schlechter mystacidii (Reichb.f.) Schlechter verdickii (De Wild.) Schlechter	(Z) (MS) (N; MS; SS) (Z; MS; LM) (Z; MS)
Rangaeris (Schlechter) Summerh. muscicola (Reichb.f.) Summerh.	(Z; MS)
Ypsilopus Summerh. longifolia (Kraenzl.) Summerh.	(MS)
Cyrtorchis Schlechter arcuata (Lindl.) Schlechter glaucifolia Summerh. praetermissa Summerh.	(Z; MS; LM) (N) (Z; MS)
Solenangis Schlechter aphylla (Thou.) Summerh.	(Z; LM)
Angraecopsis Kraenzl. amaniensis Summerh. parviflora (Thou.) Schlechter	(N; T) (N; Z; MS)
Tridactyle Schlechter anthomaniaca (Reichb.f.) Summerh. (syn. Angraecum trachyrhizum Schlechter)	(Z; MS)
inaequilonga (De Wild.) Schlechter bicaudata (Lindl.) Schlechter teretifolia Schlechter tricuspis (Bol.) Schlechter tridactylites (Rolfe) Schlechter	(MS) (N; MS) (MS) (T) (N; Z; MS)

REFERENCE

tridentata (Harv.) Schlechter

SCHELPE, E. A. C. L. E., 1965. Orchids in Northern Mozambique. *Am. Orchid Soc. Bull.* 34: 1076–1082.

(Z; MS)

EMBRYOLOGY OF ERYTHRINA CAFFRA THUNB.: SPOROGENESIS AND GAMETOGENESIS

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ABSTRACT

Microsporogenesis takes place in tetrasporangiate anthers. Microspore tetrads are tetrahedral. The tri-porate microspores are two-celled at the time of shedding. Ovules are bitegmic and crassinucellate. The megaspore tetrads are typically linear and development of the female gametophyte is of the *Polygonum*-type.

UITTREKSEL

EMBRIOLOGIE VAN *ERYTHRINA CAFFRA* THUNB: SPOROGENESE EN GAMETOGENESE

Mikrosporogenese vind in tetrasporangiate helmknoppe plaas. Mikrospoortetrades is tetrahedraal. Die mikrospore besit drie porië en is met vrystelling tweesellig. Saadknoppe besit elk twee integumente en is krassinusellêr. Die megaspoortetrades is tipies liniêr en die ontwikkeling van die vroulike gametofiet vind volgens die *Polygonum*-tipe plaas.

Introduction

Erythrina caffra, an indigenous papilionaceous tree, is distributed along the coastal districts of the eastern Cape Province, the lower Natal south coast and Zululand (Hennessy, 1972). Its occurrence in the Alexandria forest is frequent and some specimens attain heights of 18 to 20 metres (Batten & Bokelmann, 1966; Hennessy, 1972). E. caffra is commonly cultivated in gardens and parks. Despite its recognition as an ornamental, E. caffra has been botanically neglected. This paper deals with an investigation of its sporogenesis and gametogenesis. The embryology of E. caffra has not yet been described, although a similar study has been conducted on E. indica (syn. E. variegata var. orientalis) by Chandravadana (1963).

MATERIAL AND METHODS

The material for this study was collected from a tree on the Bird Street Campus of the University of Port Elizabeth. Anthers and ovaries were fixed in Craf II (Sass, 1958). Dehydration was carried out in an ethyl alcohol/tertiary butyl alcohol series. The tissue was embedded in paraffin wax (55°C) and sectioned at 10 μ m on a rotary microtome as prescribed by Brooks, Bradley and Anderson (1950). Staining materials included safranin-fast green (Holtzhausen, 1972) as well as safranin-haematoxylin (Brooks *et al.*, 1950).

RESULTS AND DISCUSSION

The anther

Initially the anther of *E. caffra* consists of a mass of uniform meristematic cells surrounded by an epidermis. Eventually four pollen sacs become evident (Fig. 1) and as the anther matures the septum in each lobe breaks down.

The anther has a distinct and persistent epidermis (Fig. 1), which remains simple and uniseriate. Below this is the endothecium, easily recognisable because of its horseshoe-shaped fibrous thickenings (Fig. 1). Surrounding the sporogenous cells are the uninucleate cells of the tapetum. These are of the glandular or secretory type as defined by Maheshwari (1950). Between the endothecium and the tapetum are one to three middle layers. These are ephemeral and in later development of the anther, appear somewhat obliterated.

Microsporogenesis

The primary sporogenous cells, after mitotic divisions, give rise to the microspore mother cells (Fig. 2). These then divide meiotically to produce microspore tetrads. Microsporogenesis occurs simultaneously and the tetrads are typically tetrahedral (Fig. 3). Each tetrad is enveloped by a thick callose layer.

Microgametogenesis

The pollen grains of *E. indica* are reported to be more or less spherical and typically triporate (Chandravadana, 1963). Those of *E. caffra* resemble this closely (Fig. 4). The exine is conspicuous and characteristically thickened. According to Davis (1966) the pollen grains of papilionaceous legumes may have two or three nuclei by the time they are shed. In *E. indica*, Chandravadana (1963) reports the presence of two nuclei. Pollen grains of *E. caffra* are also two-celled at the time of shedding.

The ovule

The short-stalked ovule of *E. caffra* is campylotropous and bitegmic (Fig. 5). At the megaspore mother cell stage the outer integument alone forms the micropyle (Fig. 6). However, by the time the embryo-sac is mature, the inner integument also participates in micropyle formation. In *E. indica*, the bitegmic condition also exists and both integuments are responsible for the formation of the micropyle. (Chandravadana, 1963).

While the ovule is still young the inner integument is two cell layers thick and the outer integument consists of three cell layers (Fig. 6). Later, however, the outer integument becomes multiseriate.

At the micropyle is a "plug" of tissue inserted between the lips of the outer integument (Fig. 5). This is an extension of the inner integument and seems to answer to the description of an operculum (Kapil & Vasil, 1963).

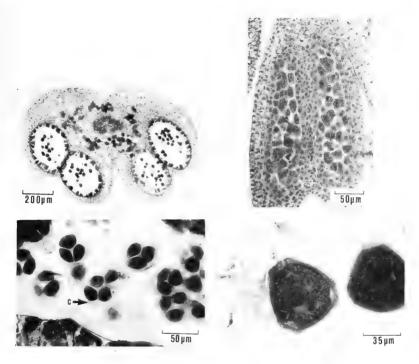


FIG. 1. A transverse section through an anther showing the four sporangia.

 $$\operatorname{Fig.}\ 2$.}$ Longitudinal section through a young anther showing microspore mother cells.

 $F_{IG},\ 3.$ Microspore tetrads with typical tetrahedral disposition (c = callose layer).

Fig. 4. A triporate pollen grain of *E. caffra*.

The megaspore mother cell of *E. caffra* is separated from the nucellar epidermis by a layer of cells and is also flanked by parietal tissue (Fig. 6). According to the definitions of Maheshwari (1950) and Eames (1961), ovules of this type are crassinucellate.

The vascular supply of the ovule consists of a single funicular bundle which terminates in the chalazal region.

Megasporogenesis

The megaspore mother cell (Fig. 6) undergoes meiosis. After the first division a dyad is formed (Fig. 7) and the two nuclei are separated by a transverse wall. As a result of the second division a tetrad forms (Fig. 8). In *E. caffra* the tetrads are typically linear, although T-shaped tetrads were also observed. The three megaspores at the micropylar end degenerate, leaving only the chalazal megaspore to function and eventually give rise to the embryo-sac (Fig. 8).

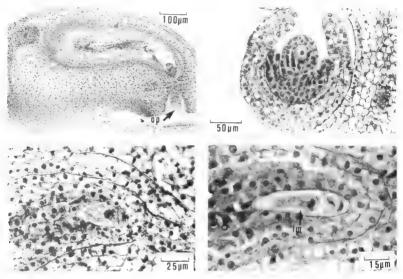


Fig. 5. A longitudinal section through the campylotropous ovule (op = operculum).

Fig. 6. A transverse section of the bitegmic, crassinucellate ovule showing the megaspore mother cell

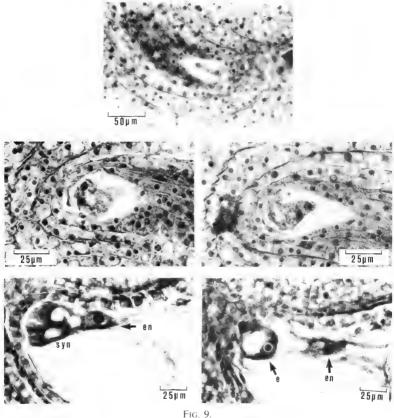
Fig. 7. The megaspore dyad after the first division of the mother cell.

Fig. 8. A tetrad showing two degenerating micropylar megaspores and the single functional megaspore (fm) at the chalazal end.

Megagametogenesis

The functional megaspore (Fig. 8) enlarges and then divides mitotically to form two nuclei which migrate to opposite poles of the embryo-sac (Fig. 9). Each of these nuclei divides again to produce a four-nucleate embryo-sac (Fig. 10a & b). After a third division the elongated embryo-sac contains eight nuclei. Four of

these, aggregated at the micropylar end, constitute the three-celled egg apparatus (Fig. 11a & b) and one of the polar nuclei. The four chalazal nuclei differentiate to form the second polar nucleus and the three antipodals. The two spherical polar nuclei are equal in size and shape and fuse prior to fertilization to form the primary endosperm nucleus (Fig. 11a & b).



A longitudinal section through the ovule showing a binucleate embryo-sac.

FIG. 10.

A longitudinal section of the four-nucleate embryo-sac of $E.\ caffra$ showing (a) the chalazal and (b) the micropylar nuclei.

FIG. 11a.

Mature embryo-sac showing the primary endosperm nucleus (en) and the synergids (syn). Fig. 11b.

Mature embryo-sac showing the egg cell (e) and the primary endosperm nucleus (en).

In *E. caffra* the embryo-sac development is monosporic and follows the pattern of the *Polygonum*-type. Megasporogenesis and the development of the embryo-sac correspond to the findings reported for *E. indica* (Chandravadana, 1963).

Organization of the mature embryo-sac

Each of the synergids of *E. caffra* has a large vacuole at its chalazal end and a nucleus at the micropylar end (Fig. 11a). No hooks or filiform apparatus are present. In *E. indica*, however, the synergids do possess hooks (Chandravadana, 1963). Their degeneration occurs before fertilization.

The antipodals are typically triangular in shape and these, too, are ephemeral, degenerating before the synergids. Within the embryo-sac and concentrated round the primary endosperm nucleus is cytoplasm with an exceptionally granular appearance, which suggests the presence of starch grains.

In general the results of this study are in accordance with those previously published for legumes and, in particular, for *E. indica* (Chandravadana, 1963).

ACKNOWLEDGEMENTS

This paper forms part of a project which was financially supported by the C.S.I.R., Pretoria and the University of Port Elizabeth.

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STUDIES IN THE BULBOUS LILIACEAE IN SOUTH AFRICA: 6. THE TAXONOMY OF *MASSONIA* AND ALLIED GENERA

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ABSTRACT

The history of taxonomic work on Massonia (Liliaceae) and allied genera is outlined. Keys to the genera and species dealt with are provided. In the main part, there is a full taxonomic treatment of Massonia (eight species), Polyxena (two species), Daubenya (one species), Androsiphon (one species), Amphisiphon (one species) and Whiteheadia (one species). The most important proposed alterations to previous generic concepts are the inclusion of the Cape species of Hyacinthus in Polyxena and the incorporation of part of Polyxena (a group recognized formerly as Neobakeria Schltr.) into Massonia. At the specific level a very considerable reduction in the number of species is proposed.

UITTREKSEL

STUDIES VAN DIE BOLDRAENDE LILIACEAE IN SUID-AFRIKA: 6. DIE TAKSONOMIE VAN MASSONIA EN VERWANTE GENERA

Die geskiedenis van die taksonomiese werk op Massonia (Liliaceae) en verwante genera word geskets. Sleutels word voorsien vir die genera en soorte wat behandel word. Massonia (agt soorte), Polyxena (twee soorte), Daubenya (een soort), Androsiphon (een soort), en Whiteheadia (een soort) word taksonomies volledig behandel. Die belangrikste voorgestelde wysigings aan vroeëre generiese begrippe is die insluiting van die Kaapse soort van Hyacinthus in Polyxena en die toevoeging van 'n gedeelte van Polyxena ('n groep reeds erken as Neobakeria Schltr.) tot Massonia. 'n Aansienlike aantal minder soorte word voorgestel.

Introduction

In a previous paper (Jessop, 1975) it was proposed that twelve genera should be included in a tribe – the Massonieae. Within this tribe, *Massonia, Neobakeria, Polyxena, Hyacinthus* (Cape species only), *Daubenya, Androsiphon, Amphisiphon* and *Whiteheadia* appear to comprise a natural group. Although this group cannot be defined by any features characterizing the group as a whole, the genera are not separated from one another by very considerable differences. This group of genera is in need of revision at both generic and specific level, and is the subject of this paper. They are referred to in this paper as the ''Massonia group''.

TAXONOMIC HISTORY OF THE MASSONIA GROUP

In 1753, Linnaeus described *Hyacinthus*, but it was not until 1771, in his *Mantissa*, that he described a South African species – *H. corymbosus*. Although

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this species was transferred by Ker-Gawler first to *Massonia* in 1807 and then to *Scilla* in 1812, and by Kunth to *Periboea* in 1843, most authors have, until the present, continued to treat it as correctly assigned to *Hyacinthus*.

The next genus in this group to be described was *Massonia*, which was described by Houttuyn in 1780, based on a manuscript name proposed by Thunberg. Its affinities were not discussed.

In the nineteenth century three further genera were described. Of these, Whiteheadia has always been regarded as monotypic. Prior to Harvey's (1868) erection of a new genus for it, this species had been variously placed in Eucomis, Basilaea and Melanthium, but Harvey's opinion has not since been challenged. Daubenya was described in 1835 by Lindley for a newly discovered species and his decision, too, has never been queried. A further two species have been described. Hall (1970) has recently suggested that the genus be treated as monotypic. The third genus, Polyxena, is larger in terms of species and more complex in its relationships. It was described by Kunth (1843) for a species previously placed by Jacquin in Polyanthes. Species have been transferred to Polyxena from Mauhlia, Agapanthus, Massonia and Hyacinthus. Baker (1896–7) recognized ten species, but since then a further four epithets have been included.

Baker (1896–7) recognized five genera in the group treated in this paper – Daubenya, Hyacinthus, Massonia, Polyxena and Whiteheadia. He placed Massonia and Daubenya in the tribe Allieae on the basis of their "umbel, which is subtended by a spathe of 1–2 or more membranous bracts". This description is based on a very superficial resemblance to the inflorescence of other members of the Allieae. A better description would probably be a raceme with a very short axis and with large, often showy, sterile lower bracts. The pedicels are clearly individually subtended by the fertile bracts. The two genera were distinguished from one another on the basis of the "regular perianth limb" of Massonia and "irregular perianth limb" of Daubenya. The remaining three genera were placed in the tribe Scilleae. Whiteheadia was distinguished from Polyxena by having a short perianth tube and connate filaments – in Polyxena the tube is cylindrical and the filaments free. His reasons for distinguishing Hyacinthus from these two are not apparent to the present author.

A further three genera have been described this century. In 1924 Schlechter published two new genera – Androsiphon and Neobakeria. The former he considered to have affinities with Massonia, but to be clearly distinct because of the staminal tube which he referred to as a gynostegium. Schlechter recognized a single species of Androsiphon and no further combinations have been made. Baker (1896–7) had recognized two subgenera in Polyxena. Subgenus Astemma, consisting of six species, was recognized by Schlechter as sufficiently distinct to justify its erection to generic status (as Neobakeria). Barker (1936) described Amphisiphon – a further monotypic genus. She linked it with Androsiphon on the basis of its long staminal tube. It differs in having a long perianth tube and in

lacking a disc at the distal end of the staminal tube. The capsule differences seem to be especially important; "that of *Androsiphon* being obovate, sharply angled at the top, leathery and dehiscing loculicidally, whereas in *Amphisiphon* the roundly angled membranous capsule is broadest at the base, and narrows gradually into the long persistent style, an unusual character within this group of genera, so far as known. In dehiscence the fruit drops from the pedicel, the three carpels then separate from the base upwards and finally each splits down the septum".

Table 1 – Generic characters in the *Massonia* group employed by Hutchinson (1959), Krause (1930) and Phillips (1951).

Genus	Hutchinson	Krause	Phillips
Hyacinthus	Flowers not in heads. Ovules few.	Leaves several.	Filaments free. Inflorescence not a
Polyxena	Flowers not in heads. Ovules numerous. Filaments free.	Bracts all fertile. Filaments free. Leaves few.	Inflorescence a corymb. Stamens in 2 rows. Filaments connate at base (in key); free or connate (in text).
Whiteheadia	Flowers not in heads. Ovules numerous. Filaments connate at base.	Bracts all fertile. Filaments connate. Leaves paired.	Inflorescence a dense subspicate raceme. Stamens in 1 row. Filaments connate at the base. Perianth segments longer than the tube.
Massonia	Flowers in umbel-like heads. Perianth actinomorphic. Stamens longer than the perianth.	Lower bracts sterile. Filaments free. Leaves paired.	Filaments united at base into a cup. Flowers regular.
Daubenya	Flowers in umbel-like heads. Perianth oblique. Stamens shorter than the perianth.	Lower bracts sterile. Filaments connate in a ring. Leaves paired.	Filaments free. Outer flowers bilabiate.
Androsiphon	Flowers not in umbel- like heads. Ovules numerous. Filaments connate in a long tube.	Lower bracts sterile. Filaments connate in a tube. Leaves paired.	Filaments united into a tube. Flowers regular.
Neobakeria	Not recognized.	Not recognized.	Inflorescence a lax raceme or shortly peduncled raceme or sometimes the raceme head-like. Perianth segments shorter than tube. Stamens in 1 row. Filaments connate at the base.

Krause (1930), Hutchinson (1959) and Phillips (1951) provide the most important reviews of the genera of the Liliaceae since Baker (1896–7).

Krause recognized six genera in the *Massonia* group – all that had been described at that time except *Neobakeria* which was treated as a synonym for *Polyxena*. He included them all within a single tribe – Scilloideae. The characters he used in his key for distinguishing these genera are summarized in Table 1.

Hutchinson regarded *Neobakeria* as a synonym for *Polyxena* and placed *Amphisiphon* under *Androsiphon*. *Massonia* and *Daubenya* were placed in a tribe Massonieae (with only two genera) on the grounds of their having their flowers "not in heads or umbel-like heads". The remaining genera were included in the Scilleae. The characters used are summarized in Table 1.

Phillips recognized all the described genera, except *Amphisiphon*, which he included under *Androsiphon*. Phillips was one of the few authors who have recognized *Neobakeria*. For characters used in his key see Table 1.

Krause (1930), Airy Shaw (1966) and Phillips (1951) attempted to estimate the numbers of species in each genus, as indicated in Table 2.

DISCUSSION OF GENERIC CHARACTERS

Massonia (sensu Phillips, 1951; Hutchinson, 1959 and Krause, 1930) is characterized by being bulbous, with actinomorphic flowers arranged in an umbel-like head, and with the inflorescence surrounded by more or less showy spathe-like sterile lower bracts. Polyxena and Neobakeria differ according to the former two authors in having racemose or corymbose inflorescences and, according to Krause, in having the lowest bracts fertile.

The *Massonia* inflorescence is typically a contracted raceme, and a series of specimens provides a continuous gradation from this form to the type characterizing *Polyxena* and *Neobakeria*. Similarly, a range of intermediates links those specimens of *Massonia*, with conspicuous spathe-like bracts, with specimens completely lacking these structures. It is, therefore, considered by the present

Table 2 - Species numbers	estimated by Krause	(1930),	Airy Shaw	(1966)
	and Phillips (1951).			

Genus	Krause	Airy Shaw	Phillips
Androsiphon Amphisiphon	1	1	2
Daubenya Hyacinthus	1	1 30	1 75
,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		(did not specify S. Afr. spp.)	(2 S. Afr.)
Massonia	30	45	45
Neobakeria	8	9	10
Polyxena Whiteheadia	10–12 1	10	10 1

author that neither of these characters affords suitable criteria for distinguishing these genera.

However, several other characters are of possible value. There is a pattern of leaf structures which is apparently characteristic of *Polyxena* (and also occurring in *Lachenalia* and the Cape species of *Hyacinthus sensu* Phillips). In these groups, between each cycle of vegetative leaves there is an intermediate, generally lamina-less membranous leaf forming a tubular sheath round the proximal part of the leaves, and projecting a short distance above the bulb. This structure is not always detectable on herbarium material (although it usually is), but is thought likely to be a constant feature of *Polyxena sensu stricto*, certainly is of *Hyacinthus* (Cape species only), and has never been observed in *Massonia* or *Neobakeria*. Baker (1896–7, p. 419) stated "I have followed Mr Bentham in classification, but my own view would be to unite, at any rate, the subgenus *Astemma* [i.e. *Neobakeria*] with *Massonia*". Although he did not elaborate on this point, it is clear, therefore, that Baker recognized that *Neobakeria* is closer to *Massonia* than to *Polyxena*.

A second feature of possible generic significance is the insertion of all the filaments at one level on the perianth in *Massonia* and *Neobakeria*, but at two distinct levels in *Polyxena* (sensu stricto) and *Hyacinthus* (Cape species).

The close correlation between the bulb and filament characters has led the present author to the decision to unite *Massonia* and *Neobakeria* (under the older name – *Massonia*), but to retain *Polyxena* as a separate genus.

The Cape species of *Hyacinthus* share the above-mentioned characters with *Polyxena*, and it is necessary to re-examine the characters by which they are separated. The following are the characteristics used in recent keys: Krause (1930) stated that *Hyacinthus* had several leaves and *Polyxena* only 2–5. Hutchinson (1959) stated that *Hyacinthus* had few ovules and *Polyxena* numerous ovules. Phillips (1951), in his key, stated that *Hyacinthus* had free filaments and *Polyxena* connate filaments. *Polyxena* has free filaments and Phillips' use of this character need not be considered. In the generic description, Phillips acknowledged the occurrence of both free and connate filaments in *Polyxena*.

Polyxena and Hyacinthus have a similar number of ovules, usually 10–20. Polyxena usually has only two leaves, but occasionally more. Hyacinthus occasionally has as few as two leaves. In practice these two genera are readily separable as Hyacinthus has narrower leaves and fewer flowers, but these are considered by the present author to be specific rather than generic differences.

The geographical distribution of *Hyacinthus* is, perhaps, also relevant. The genus is almost entirely restricted to the northern hemisphere. The Cape species are, therefore, extremely isolated from the majority of the species. While this may represent an example of a similar phenomenon to that exhibited by *Viola* (Jessop, 1967), the degree of isolation is greater with no other species known to the present author from south of the Sahara.

It is, therefore, proposed that the Cape species of *Hyacinthus* be placed in *Polyxena*.

The remaining genera in the *Massonia* group are more readily definable. The characters employed by previous authors are believed to be accurately recorded and appropriate. *Daubenya*, *Androsiphon*, *Amphisiphon* and *Whiteheadia* are recognized and regarded as monotypic. *Amphisiphon* is separated from *Androsiphon* on the characters pointed out by Barker (1936).

KEY TO THE GENERA IN THE MASSONIA GROUP

Filaments connate at the base Inflorescence elongate; flowers green and succulent
Filaments fused to perianth tube at mouth Filaments fused to form a tube under 10 mm long Massonia Filaments free at the base
Flowers (or at least the lower) zygomorphic
Bulb with a distinct tubular membranous sheath surrounding the base of the aerial parts

1. Massonia Houtt. Natuurl. Hist., pt. 2, 2: 424 (1780).

Neobakeria Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924). Type species not designated.

Bulb usually with membranous outer scales, rather small – generally less than 35 mm long; scales tubular, all fleshy. Leaves almost always two, often spreading - often tightly adpressed to the ground - often rather broadly oblong or elliptic, less often lanceolate or narrowly oblong to orbicular, glabrous, ciliate, or with simple trichomes varying from pustules to firm bristles. Peduncles usually solitary, producing a very condensed subcapitulate raceme close to ground-level. Inflorescence usually surrounded by large sterile bracts, which are usually more or less green or with a reddish colour; upper bracts very much smaller. Flowers actinomorphic, pedicellate, usually pink, white or green, less often yellow to red. Perianth fused to form a tube which usually completely surrounds the ovary and may be several times as long as the ovary, marcescent, leaving a distinct scar at the base of the young fruit, adhering to the apex of the young fruit; the free segments more or less oblong, usually with a sigmoid folding in the longitudinal axis towards the base, often minutely papillate at the apex. Stamens all usually the same length, attached at the mouth of the perianth tube; filaments free, connate at the base only, or fused for most of their length; sublinear to narrowly deltoid; anthers dorsifixed, oblong to linear, straight or slightly arcuate. Ovary sessile, oblong, ellipsoid or ovoid; each carpel containing several axile ovules (often c. 15–25). *Style* sublinear, usually slightly longer than the stamens. *Stigma* subcapitate to undifferentiated. *Fruit* a loculicidal, winged or deeply lobed capsule, containing numerous black subglobose seeds about 1–2 mm in diameter. Flowers usually pleasantly scented and producing copious nectar.

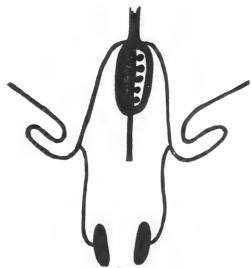
Type: M. depressa Houtt.

Species concepts in Massonia

As in most genera of the Scilleae, most species have been defined by previous authors on the basis of quantitative characters. Within populations there is considerable variation in the measurements of the leaves and in the number of flowers and other quantitative features. This is probably often due to flowering of comparatively young plants as well as very much older plants, as well as genetic and environmental factors. Unlike *Ledebouria* and *Drimiopsis* large quantities of seeds are produced so that there is less evidence for apomixis or other reproductive abnormalities. In selecting taxonomic characters for distinguishing species every effort has been made to employ qualitative characters where possible. The following characters are probably the more important:

- (1) Leaf characters: whether the leaves are flat on the ground or more or less erect is generally constant in populations, but some variation does occur. The size and shape of leaves is not reliable except within very wide limits. This aspect is dealt with under individual species. Trichomes afford a number of characters of potential value which have been used by previous authors. They vary from coarse bristles or other types of hairs to pustules, but it has been found that within populations plants otherwise similar to one another may sometimes have trichomes and sometimes not even plants with one hairy leaf and one glabrous leaf have been found. There is also a considerable gradation between most types of trichomes. The pustulate form, however, appears to be clearly distinguishable from other forms in almost all the plants examined and is used as the principal character for defining M. pustulata.
- (2) Bract characters: whether or not sterile lower bracts (spathes of some authors) are formed has formerly been used in distinguishing the genera Massonia and Neobakeria. It has generally been found possible to distinguish species on this character, but exceptions are known where plants without these bracts are placed in species which do usually have these bracts. A coma is formed in a few plants of M. angustifolia. However, this character varies within otherwise relatively homogeneous populations.
- (3) Floral characters: in many plants there is a very pronounced folding of the proximal part of the perianth segments so as to form a curve, referred to in the text as a sigmoid curve (Fig. 1). Although intermediates between this form and plants with straight, erect or spreading perianths have not been found, it does not show a strong association with other characters. It is, therefore, not used here as a specific character. Although species, such as M. depressa sometimes have it, but not

always, there are species, such as M. angustifolia, which probably never show this character.



Half flower of *Massonia depressa* to show curve in perianth segments.

KEY TO THE SPECIES OF MASSONIA

- - minutely ciliate margin.

 4 Perianth tube more than 5 mm long, more or less cylindrical 1. depressa
 4a Perianth tube less than 5 mm long, more or less cup-shaped 2. grandiflora
 - 3a Anthers usually less than 2 mm long or, if more, then the leaves hairy or papillate.

 - 5a Filaments usually all of the same length in each flower; leaves glabrous, hairy or pustulate and usually more than 30 mm long.

 - 6a Leaves often hairy or pustulate; filaments usually free or with the free part more than 3 mm long; perianth segments usually approximately the same length as the tube; tube usually at least 3 mm in diameter.
 - 7 Leaves with papillae or pustules on upper surface 4. **pustulata**

1. **Massonia depressa** Houtt., Natuurl. Hist., pt. 2, **2:** 424, t.85, fig. 1 (1780). Type: "De eenigste soort, mischien, daar van tot heden bekend (Massonia Thunb.)", *?Thunberg s.n.*, not traced; Houtt., Natuurl. Hist., pt. 2, **2:** t.85, fig. 1 (1780), lecto.

Massonia latifolia L.f., Suppl. 193 (1781). Type: "Cap. bonae Spei, F. Masson"; not located.

Massonia sanguinea Jacq., Hort. Schoenbr. 4: 31, t.461 (1804). Type: South Africa without precise locality or collector, Jacq., Hort. Schoenbr. 4: t.461 (1804), lecto.

?Massonia obovata Jacq., Hort. Schoenbr. 4: 29, t.458 (1804). Type: Jacq., Hort. Schoenbr. 4: 29, t.458 (1804), lecto.

Massonia brachypus Bak. in J. Bot. 1874; 368 (1874). Type: "Caput Bonae Spei, Hort. Kew., Feb., 1874" (K, holo.!, BOL, drawing!).

Massonia namaquensis Bak. in Fl. Cap. 6: 416 (1897). Type: "Little Namaqualand; near Kook Fontein, 3 000 ft.", Bolus 6596 (BOL, lecto.!; K!); Scully 27 (K!).

Massonia triflora Compton in Trans. R. Soc. S. Afr. 19: 276 (1931). Type: Whitehill Ridge, south side, Compton 3515 (BOL, holo.!).

Bulb usually ovoid, (17–) 20–30 (–45) mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, orbicular to oblong, acute or apiculate, flat on the ground, coriaceous to fleshy, glabrous, rarely ciliate on margins, sometimes with conspicuous longitudinal grooves, (50–) 70–150 (–260) mm long, 40–100 (–150) mm broad, green, with or without green or purple flecks, patches of striations. Inflorescence capitate, with often about 20-30 flowers. Lower bracts conspicuous, ovate to obovate, acute to sub-attenuate, glabrous, (15-) 30-40 (-50) mm long, 10-15 (-20) mm broad, green, often pale or reddish or purplish towards the base, or purplish with a green margin. Pedicels 5-20 mm long, rather thick. Perianth green, yellow, white, cream, pink to red (especially in the tube) or brown, occasionally flecked with purple; tube (5-) 10-15 (-17) mm long, (2-) 4-6 (-8) mm broad at mouth, narrowing slightly to base; segments oblong, slightly broader at base, usually with a sigmoid curve in the longitudinal axis towards the base, (7-) 8-10 (-12) mm long. Filaments (8-) 10-16 (-18) mm long, connate portion at base up to 1-2 mm long, linear-lanceolate, often cream, yellow or green, less often purplish; often red or purple in the tube, with yellow or purple anthers which are (2-) 2,5-4 mm long. Style 10-14 mm long. Ovary obovoid, with up to 30 ovules per locule; septa at least sometimes hollow. Capsule obovoid 3-winged, emarginate, (10-) 15-20 (-30) mm long.

Widespread in the Cape Province except the eastern parts.

Occurs in a range of habitats in shade and in the open. Frequent on both sandy flats and rocky slopes. Flowers are produced in winter, with a strong peak in July



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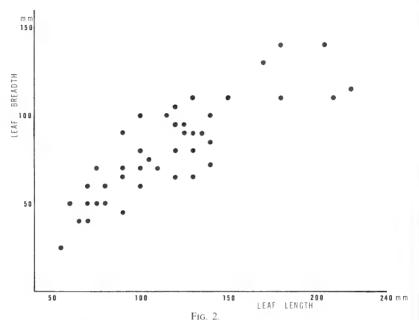


Diagram to indicate variation in leaf measurements in Massonia depressa. From herbarium material.

and August. There appears to be no correlation between geographical distribution and flowering times – climatic variation probably being significant, however.

Usually scented and producing copious nectar.

Leaf measurements are very variable, but as indicated in Fig. 2 there appears to be no likelihood that overall measurements could provide characters for subdivision of the species. Fig. 3 shows variation in a population.

Houttuyn's figure of the flowers of *M. depressa* shows the large anthers characteristic of the present concept of this species. As he made no reference to surface characters of the leaves, it seems likely that his specimen had glabrous leaves and that Houttuyn's epithet is correctly applied here. Houttuyn ascribed the generic name to Thunberg, but the binomial does not appear in the Thunberg collection in Uppsala, although it is likely that Houttuyn based this species on a Thunberg specimen. The specimen has also not been traced in the Rijksherbarium, Leiden. Two specimens identified as *M. latifolia*, either of which could possibly be the one on which Houttuyn based his description, are known. In the Linnaean Herbarium, London, there is a specimen labelled, according to Savage (1945): "414.1 Massonia (m.L.) latifolia (m.Lf.)". If this is a correct identification of the

script, then Linnaeus, the elder, may deserve the credit for commemorating Masson's name, but there is no evidence that Masson collected the plants on which this name was based. However, in 1781, Linnaeus the younger described *M. latifolia*, based on a Masson specimen. Both Houttuyn and Linnaeus compared the plant with a *Haemanthus*, but whereas Houttuyn described the leaves as "ovaalachtig", Linnaeus called them "orbiculati". Linnaeus, but not Houttuyn, referred to the capsules, and it is probable that these two authors were referring to different specimens. The Thunberg (UPS) specimen of *M. latifolia* is in fruit and can, therefore, not be regarded as the type. The figure accompanying the type description has been selected as the lectotype. There is a specimen, collected by Masson, in Geneva (G), but this is of *M. echinata*.

Typification of *M. latifolia* is similarly complicated by the failure to trace a specimen definitely collected by Masson, other than the one mentioned above of

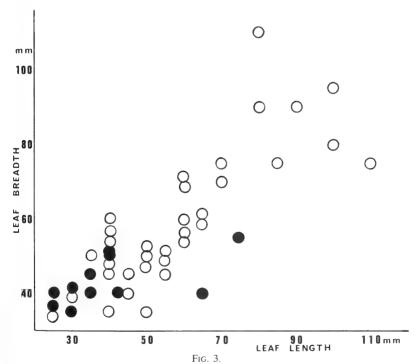


Diagram to illustrate variation in a population of plants resembling *Massonia depressa* in having anthers at least 2 mm long. Population area: top of Van Rhyn's Pass (3319; Calvinia, Cape). Solid spots indicate muricate leaves. Open dots indicate smooth leaves.

M. echinata. The type description of M. latifolia described the plant as "Massonia foliis orbiculatis glabris", which makes it very likely that the name is correctly placed in synonymy under M. depressa. Baker (1896–7) placed M. depressa in synonymy under M. latifolia.

The assigning of two of Jacquin's epithets to this species, is based on the type descriptions and the illustrations which are barely adequate to be certain of their identity. The illustration of M. sanguinea is, however, a particularly good match for typical specimens of M. depressa.

M. latifolia sensu Ker-Gawl., Bot. Mag. 22: 848 (1805), was treated by Baker (1896–7) as not synonymous with M. latifolia L.f., but with M. sanguinea Jacq. However, Gawler did cite M. latifolia L.f. and his figure appears to be correctly assigned to this species.

The selection of the Bolus Herbarium material as the lectotype of *M. namaquensis* Bak., is because this specimen is annotated in Baker's hand.

For illustration see Flower. Pl. S. Afr. 2: t.46 (1922).

SELECTED SPECIMENS

ORANGE FREE STATE—2925 (Jagersfontein): Fauresmith Veld Reserve, *Henrici* 2793 (PRE).

CAPE—2917 (Springbok): 2 miles N. of Concordia, Rourke 811 (NBG).

- —2918 (Gamoep): 18 miles NE. of Springbok, Schlieben 9073 (PRE).
- -3017 (Hondeklipbaai): 3 miles E. of Soebatsfontein, Hall 2901 (NBG).
- -3023 (Britstown): Britstown, Loots s.n. (STE).
- -3024 (De Aar): De Aar, Friedlander s.n. (GRA).
- —3026 (Aliwal North): Ruigtefontein, Thode A1871 (NH, PRE).
- —3118 (Vanrhynsdorp): Heerenlogement, Esterhussen 5587 (BOL).
- -3119 (Calvinia): top of Botterkloof Pass, Lewis 2979 (SAM).
- -3120 (Williston): 14,5 miles E. of Calvinia, Acocks 16823 (PRE).
- —3123 (Victoria West): Murraysburg, Tyson 361 (BOL, SAM).
- —3217 (Vredenburg): Stompneus, Rourke 781 (NBG).
- -3218 (Clanwilliam): Clanwilliam, Leipoldt 270 (BOL, SAM).
- —3219 (Wuppertal): Boontjies Kloof, northern Cedarberg, Esterhuysen 12199 (BOL, NBG).
- —3220 (Sutherland): Sutherland, Stayner s.n. sub NBG 82209 (NBG).
- -3224 (Graaff-Reinet): Aberdeen Road, Du Plessis s.n. sub NH 16066 (NH).
- —3225 (Somerset East): near Mortimer, Kensit s.n. sub BOL 9251 (BOL).
- —3318 (Cape Town): Steenberg Cove, Barker 9720 (NBG).
- -3319 (Worcester): Robertson, Marloth 11943 (PRE).
- —3320 (Montagu): Whitehill Ridge, Compton 13388 (BOL, NBG).
- -3321 (Ladismith): north of Huis River Pass, Wurts 1632 (NBG).
- —3322 (Oudtshoorn): Meirings Poort, Stokoe s.n. sub SAM 63686 (SAM).
- -3323 (Willowmore): N. of Joubertina, Fourcade 2684 (BOL).
- -3326 (Grahamstown): Brake Kloof, White s.n. (GRA).

- —3419 (Caledon): near Caledon, Ecklon & Zeyher Asphod. 19 (BOL, G, HAL).
- -3420 (Bredasdorp): Bontebok Park, Grobler 573 (STE).
- -3421 (Riversdale): Riversdale, Ferguson s.n. (BOL).
- 2. **Massonia grandiflora** Lindl. in Bot. Reg. **12:** t.958 (1826). Type: "The interior of the Cape of Good Hope, brought by Mr Synnet, in Mr Colvill's nursery," Bot. Reg. **12:** t.958 (1826).

Bulb ovoid, 25–35 mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, broadly oblong to ovate, flat on the ground, fleshy, glabrous, (50–) 100–150 mm long, 40–110 mm broad, nerves depressed, dark grey-green suffused with purple, with some scattered oblong purple spots. Inflorescence capitate, with about 20–25 flowers. Lower bracts ovate, 20–30 mm long, green. Pedicels 8–10 mm long, fleshy. Perianth green to white; tube cup-shaped, 3–5 mm long, 4–6 mm broad; segments rather narrowly deltoid, 6–10 mm long, erect or reflexed, straight. Filaments 8–14 mm long, connate portion c. 2 mm long, linear-lanceolate, greenish yellow or greenish purple. Anthers brown or purple, 2–3 mm long. Style 3–5 mm long; stigma not differentiated. Ovary broadly oblong to obovoid, with numerous ovules, c. 8 mm long. Capsule obovoid, 3-winged, emarginate, c. 18 mm long.

Recorded from a few localities over a large part of the drier regions of the Cape. Flowers have been recorded in August.

Obermeyer (Flower. Pl. Afr. 37: t.1451; 1965) referred to the following features as being characteristic of *M. grandiflora* (this species has not been examined in the living state by the present author):

- (1) Fleshy, rather than delicate, perianth.
- (2) Short and wide tube.
- (3) Triangular straight segments.

The texture of the perianth cannot be determined from herbarium material, but has not been found to be consistent in living material of plants of *M. depressa* (which is its nearest ally). The short wide tube appears to be a more reliable character, but the shape of the segments of *M. depressa* is certainly not consistent. *Earp s.n.* from Murraysburg (BOL), for example, has straight segments, but a tube 8 mm long, which places it with *M. depressa*.

The isolated distant localities for this species suggest that the populations may be aberrant forms of M. depressa, but it is considered that the morphological characters suffice to separate M. grandiflora until further material clarifies its position.

For illustration see Flower. Pl. Afr. 37: t.1451 (1965).

SELECTED SPECIMENS

CAPE—2824 (Kimberley): Kimberley, Moran s.n. (GRA).

- -2917 (Springbok): Steinkopf, Meyer s.n. sub STE 12384 (STE).
- -3224 (Graaff-Reinet): Graaff-Reinet, Francis s.n. (GRA).

—3225 (Somerset East): Cranemere, Pearston, *Jenkins s.n.* sub PRE 29302 (PRE).

3. Massonia echinata L.f., Suppl. 193 (1781). Type: "Cap. bonae spei, Thunberg" (UPS – 7988, holo., microfiche!).

Massonia scabra Thunb., Prodr. 188 (1800). Type: Cape, without further locality, Thunberg s.n. (UPS – 7992, holo., microfiche!).

Massonia muricata Ker-Gawl. in Curtis's bot. Mag. 16: t.559 (1802). Type: "our drawing was made in the garden of Ed. Woodford, Esq.", Curtis's bot. Mag. 16: t.559 (1802).

Massonia scabra Andr., Bot. Rep. 4: t.220 (1802). Type: "introduced to Britain, in the year 1796, by Messrs. Lee and Kennedy", Bot. Rep. 4: t.220 (1802), nom. illegit., non Thunb.

Massonia longifolia Jacq. var. candida Burch. ex Ker-Gawl. in Bot. Reg. 9: 694 (1823). Type: "Raised at Mr Colvill's nursery from a plant that had been raised two years before from seed from Mr Burchell"; "Little Brak River, Mossel Bay Div.", Burchell 5746 (K, lecto.!).

Massonia candida Burch. ex Kunth, Enum. Pl. 4: 297 (1843), nom. nud.

Massonia candida Burch. ex Bak. in Fl. Cap. 6: 415 (1897). Type: Little Brak River, Burchell 6197/5 (K, holo.!).

Massonia hirsuta Link & Otto, Icon. Pl. Rar. 1: t.1 (1828). Type: Type description not located. Baker (1896/7) cited Masson s.n., Zeyher 4273 and Ecklon & Zeyher 130. (Ecklon & Zeyher 130, TCD!) The choice of epithet places this species with a high degree of probability.

Massonia pygmaea Schlechtdl. ex Kunth, Enum. Pl. 4: 298 (1843). Type: "Cap. b spei", Mund & Maire s.n. sub HAL 33934 (HAL!).

Polyxena bakeri (Schlechtdl. ex Kunth) Dur. & Schinz, Consp. Fl. Afr. 5: 366 (1895), nom. nov. for M. pygmaea.

Massonia huttonii Bak. in J. Linn. Soc., Bot. 11: 389 (1871). Type: "Cap. b spei", Masson s.n. (BM, lecto., BOL, drawing!); Drège 3509 (K, BOL, drawing!).

Massonia setulosa Bak. in J. Linn. Soc., Bot. 11: 389 (1871). Type: "Cap. b spei", Ecklon & Zeyher s.n. (TCD, holo.!).

Massonia versicolor Bak. in J. Bot., Lond. 1876: 184 (1876). Type: "C.B.S. in argillaceis apricis fluminis Klyn Visch rivier, alt. 2 500 pedes". MacOwan 2178 (K, holo.).

Massonia calvata Bak. in J. Bot., Lond. 1878: 321 (1878). Type: "Cape Colony, eastern district", Bolus 749 (K, holo.).

Massonia orientalis Bak. in J. Bot., Lond. 1878: 321 (1878). Type: "Cape Colony on sand-dunes at Port Elizabeth", Bolus 2239 (not located).

Massonia latebrosa Masson ex Bak, in J. Bot., Lond. 1886: 336 (1886). Type: "Bokveld, Aug. 1792", Masson s.n. (BM, drawing, holo., BOL, copy!). A Masson specimen, without locality, in G matches the BM drawing.

Massonia amygdalina Bak. in Gdnrs' Chron. 1889, 6: 715 (1889). Type: plant cultivated by Sir C. W. Strickland (K, holo., BOL, drawing!).

Massonia parvifolia Bak. in Engl. Bot. Jahrb. 15, Beih.3: 8 (1892). Type: "Cap. b spei", Ecklon & Zeyher Asphod. 25 (B, holo.!).

Massonia dregei Bak. in Fl. Cap. 6: 412 (1897). Type: "Clanwilliam Div., Lange Vallei", Drège 2688 (K, holo., BOL, drawing!; G!; HAL!; L!).

Massonia concinna Bak. in Fl. Cap. **6:** 414 (1897). Type: "Stockenstrom Div.; stony ground above the waterfall, Elands River", Scully 54 (K, holo., BOL, drawing!; SAM!).

Massonia bolusiae Barker in Flower. Pl. S. Afr. 11: t.429 (1931). Type: "The farm Bangor near Middelburg", Miss Pamela Bolus s.n. sub BOL 19615 (BOL, holo.!).

Massonia modesta Fourc. in Trans. Roy. Soc. S. Afr. **21:** 79 (1932). Type: "Div. Humansdorp: Karreedouw", *Jeppe s.n.* sub Fourcade 4592 (BOL-Fourcade collection, holo.!).

Neobakeria visserae Barnes in J. Bot. 71: 72 (1933). Type: Lamberts Bay, Visser s.n. sub BOL 19616 (BOL!).

Massonia inexpectata V. Poelln. in Portug. Acta Biol., ser. B. 1: 384 (1947). Type: locality and collector unknown "in Herbar Breslau". Not located.

Massonia bokkeveldiana V. Poelln. in Portug. Acta Biol., ser. B, 1: 384 (1947). Type: "Onder Bokkeveld", Schlechter 10935 (BOL!; G!; GRA!; PRE!).

Bulb usually ovoid, (5-) 10-20 (-40) mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, ovate to oblong, acute or obtuse, usually flat on the ground, coriaceous to fleshy, usually hairy or at least ciliate on the margins, sometimes with conspicuous longitudinal grooves, (15–) 20-80 (-150) mm long, 10-60 (-130) mm broad, often subpetiolate with the narrow basal part up to 25-50 mm long, green, often with darker green or purplish flecks, patches or striations. *Inflorescence* capitate, with (3–) 5–20 (–25) flowers. Lower bracts conspicuous, ovate to obovate, glabrous to hairy, 10–20 (–30) mm long, 5-10 mm broad, green, sometimes marked with red or purple. Pedicels 4–8 (–12) mm long. *Perianth* yellow, white or, especially in older flowers, pink; tube (4-) 5-7 (-16) mm long; segments oblong to narrowly lanceolate, with or without a sigmoid curve in the longitudinal axis towards the base, 4-8 (-9) mm long. Filaments sublinear or narrowly conical, free or shortly connate, 4-8 mm long, 0,75–1,5 mm broad at the base; anthers 0,5–1,25 mm long, yellow or purple. Style 5-10 mm long. Ovary obovoid. Capsule c. 12-40 mm long, narrowly obovoid, emarginate, usually (?always) with 3 wings well developed.

Widespread in the Cape Province.

Recorded from open sandy areas, clay soils and rock crevices, but rarely found in shade. Flowers are often sweetly scented.

Flowering is in winter, with a peak in May, June and July. It does, therefore, flower before *M. depressa*, although there is some overlap.

M. echinata, as defined in this work, includes many of Baker's species. He used mainly types of trichomes, leaf shape and length of perianth and filaments. These, approximately 25 species, were known to him by illustrations and a total of probably fewer than 20 actual specimens altogether! Fewer than two thirds of the species he recognized were known to him by specimens from recorded localities. The present author has been unable to correlate any two of these characters or any one morphological character with geographical distribution. Further, it has been found that, in practice, these characters show continuous ranges of gradation linking all the forms. As in M. depressa, there is considerable range in the dimensions of leaves of flowering plants for this species (see Fig. 4).

M. pustulata is closely allied to M. echinata and, it might be justifiably argued, should possibly be placed in the same species. The decision to maintain two distinct species was taken because it was felt that the pustules were relatively uniform in appearance and graded into the other trichome types less than the other trichome types graded into one another and because the plants with pustules tended, on the average, to be larger than those without.

For illustration see Flower. Pl. S. Afr. 11: t.429 (1931).

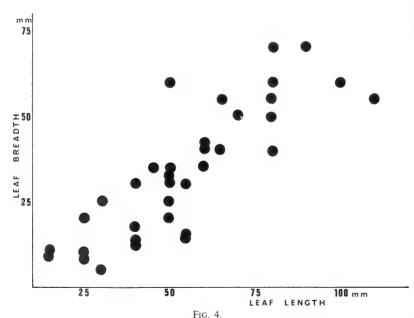


Diagram to indicate variation in leaf measurements in Massonia echinata. From herbarium material.

SELECTED SPECIMENS

- CAPE—2823 (Griekwastad): Klaarwater, Acocks 2348 (PRE).
- —3025 (Colesberg): Colesberg, Borrelkoppies, Acocks 16814 (PRE).
- -3027 (Lady Grey): Ben McDhui, Galpin 6868 (BOL, PRE).
- -3118 (Vanrhynsdorp): Mierhof, Zeyher 1717 (G, SAM).
- —3119 (Calvinia): Oorlogskloof, Schlechter 10935 (BOL, G, GRA, PRE).
- -3120 (Williston): Voelfontein, Hall 225 (NBG).
- —3123 (Victoria West): Murraysburg, Banks s.n. (BOL).
- -3124 (Hanover): Naauwpoort, Hanover, Denoon s.n. (BOL).
- -3218 (Clanwilliam): Lange Vallei, Drège 2688 (G, HAL, K, L).
- -3222 (Beaufort West): Nieuweveld Mountains, Esterhuysen 3868 (BOL).
- —3225 (Somerset East): Klein Visrivier, near Somerset East, *MacOwan 2178* (GRA).
- —3227 (Stutterheim): Prospect Siding, East London, Flanagan s.n. (PRE).
- -3319 (Wuppertal): Stettyn, Leipoldt 3779 (BOL).
- -3320 (Montagu): Langeberg Range, Wurts 195 (NBG).
- -3324 (Steytlerville): Assegaaibos, Rogers 3098 (BOL).
- -3325 (Port Elizabeth): Red House, Paterson 1115 (BOL, GRA, SAM).
- -3326 (Grahamstown): Fort Brown, Dyer 1562 (GRA, PRE).
- -3419 (Caledon): near Caledon, Bolus 8502 (BOL).
- —3420 (Bredasdorp): Bontebok Park, Acocks 22251 (PRE).
- -3421 (Riversdale): Zandhoogte, Muir 290 (BOL).
- -3422 (Mossel Bay): E. of Brak River, Fourcade 3949 (BOL).
- -3424 (Humansdorp): Humansdorp, Rogers 3098 (GRA).
- 4. **Massonia pustulata** Jacq., Collect. **4:** 177–8 (1791). Type: Jacq., Hort. Schoenbr. **4:** 454 (1804). It is thought likely that this figure was made from the same material as the type description and is selected as the lectotype or, should it be shown to be derived from other material, the neotype.

?Massonia schlechtendalii (sphalm. schlechtendahlii Baker, 1896–7) Bak. in J. Bot., Lond. 1874: 5 (1874). Type: "Cap. b. spei", Schlechtendal in Herb. DC. Although this specimen has not been traced, the type description makes it likely that it belongs in the present concept of M. pustulata.

Bulb globose or ovoid, 10–25 (–35) mm long, with whitish scales surrounded by a few, rarely up to 20, firm membranous brown scales. Leaves paired, ovate to oblong, acute, flat on the ground, thin to subfleshy, sometimes with conspicuously depressed veins, pustulate (pustules not always present on both leaves, and tending to be more abundant towards the apex), often with minutely ciliate to minutely dentate margins, 30–100 (–150) mm long, 15–) 20–70 (–130) mm broad, green with or without markings in purple, red, brown or another shade of green, sometimes subpetiolate, with a narrow basal portion up to 20–30 mm long. Inflorescence capitate, with often about 15–25 flowers. Lower bracts conspi-

cuous, ovate to obovate, acute, glabrous (12–) 15– 30 (–43) mm long, 7–16 (–24) mm broad, green often with reddish areas particularly towards the margins and base. *Pedicels* (5–) 10–12 (–15) mm long. *Perianth* pink, white, yellow or greenish; tube 6–11 (–14) mm long, 3–4 (–5) mm diameter at the mouth; segments oblong, usually more or less reflexed and with a sigmoid curve in the longitudinal axis towards the base, 4,5–10 (–14) mm long, 1,5–3 mm broad. *Filaments* 4–12 (–18) mm long, free, or connate portion at base up to 1 mm long; free portion 1–1,5 mm broad, linear or narrowly deltoid, with yellow or reddish anthers 1–1,75 mm long. *Style* 10–12 (–30) mm long. *Ovary* obovoid, 5–6 (–8) mm long. *Capsule* obovoid, 3-winged, emarginate, *c*. 30–35 mm long, 12–20 mm broad.

Widespread in the Cape Province.

Occurs, generally in the open, in coastal sand with fynbos, in dry inland areas and in rich humic soils and on clay. Flowers are sweetly scented and produced in winter (June to September).

Pocock s.n. (sub Marloth 11888) (PRE), from the Cold Bokkeveld, with leaves pustulate and c. 40 mm long, is intermediate between M. pustulata and M. heterandra, but the absence of heterandry places it closer to the former.

Esterhuysen 12199, from the northern Cedarberg (PRE), Esterhuysen 10349, from Orchard, Hex River Valley (BOL) and Marloth 12087, from Matjiesfontein (PRE) have anthers 2,5 mm long, but the characteristic pustules on the leaves. The long anthers suggest a relationship with M. depressa. However, the pustules on the upper surface of the leaves are otherwise unknown in M. depressa and the specimens are, therefore, preferred in M. pustulata. There is, alternatively, the possibility that these plants are hybrids. Except for these two characters, M. depressa and M. pustulata are rather similar. The measurements given here for the capsule are taken from the only available specimen, but they suggest that the capsule may prove to be appreciably larger in this species, although measurements of almost all other morphological features of the plant are smaller.

Barker 10435, from Elands Bay (NBG), belongs to this species, but has an unusually large perianth – the tube 18 mm long and the segments 10 mm long.

For illustration (of exceptionally large specimen) see Flower. Pl. S. Afr. 23: t.915 (1943).

SELECTED SPECIMENS

CAPE—3018 (Kamiesberg): Boonste Vlei, Klipsand, Hardy 114 (PRE).

- —3119 (Calvinia): Nieuwoudtville, Thorne s.n. sub SAM 53120 (SAM).
- —3124 (Hanover): Hanover, Paterson s.n. (GRA).
- -3218 (Clanwilliam): Elands Bay, Barker 10435 (NBG).
- -3219 (Wuppertal): Packhuis Pass, Barker 9177 (NBG).
- -3225 (Somerset East): Cradock, Muller 684 (PRE).
- -3319 (Worcester): Orchard, Esterhuysen 10349 (BOL).
- -3320 (Montagu): Matjiesfontein, Marloth 5681b (PRE).

- -3322 (Oudtshoorn): Flat Rock, Wilderness, Bayliss 2954 (NBG).
- —3323 (Willowmore): Formosa, Fourcade 3733 (BOL).
- -3325 (Port Elizabeth): Drift Sands, Long 1057 (GRA).
- -3419 (Caledon): Ratel River, Compton 14768 (NBG).
- —3420 (Bredasdorp): Struis Bay, Esterhuysen 3869 (BOL).
- —3421 (Riversdale): near Still Bay, Muir 201 (PRE).
- 5. Massonia angustifolia L.f., Suppl. 193 (1781). Type: "Cap. spei," *Thunberg s.n.* (UPS, microfiche!).

Polyxena angustifolia (L.f.) Bak. in Fl. Cap. 6: 419 (1897).

Neobakeria angustifolia (L.f.) Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924).

Massonia lanceolata Thunb., Prodr. 60 (1794). Type: Cape, without precise locality, Thunberg s.n. (UPS – 7990, lecto., microfiche!).

Massonia marginata Willd. ex Kunth, Enum. Pl. 4: 299–300 (1843). Type: "Cap. b spei" in Willd. Herb. no. 6373 (B, holo., photo.!).

Polyxena marginata (Willd. ex Kunth) Bak. in Fl. Cap. **6:** 420 (1897). Baker cited M. undulata Willd. ex Kunth, Enum. Pl. **4:** 299 (1843) as the basionym, but there is no such name. However, M. marginata does appear on p. 299 of this work and M. undulata appears, therefore, to be an error for M. marginata.

Neobakeria marginata (Willd. ex Kunth) Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924).

Massonia zeyheri Kunth, Enum. Pl. 4: 298 (1843). Type: "M. lanceolata Zeyh. in herb. reg. Berol. – Cap. b spei" (?K!) – this specimen lacks a collector's number, but has been treated as type material at Kew. It does agree with the type description.

Massonia rugulosa Lichtenst. ex Kunth, Enum. Pl. 4: 299 (1843). Type: "Cap. b spei", Lichtenstein s.n. (?destroyed in B).

Polyxena rugulosa (Lichtenst. ex Kunth) Bak. in Fl. Cap. 6: 420 (1897).

Neobakeria rugulosa (Lichtenst. ex Kunth) Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924).

Massonia burchellii Bak. in J. Linn. Soc., Bot. 11: 393 (1871). Type: "Cap. b spei", Burchell s.n. (K!, BOL, drawing!).

Polyxena burchellii (Bak.) Bak. in Fl. Cap. 6: 420 (1897).

Neobakeria burchellii (Bak.) Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924).

Polyxena haemanthoides Bak. in Hook., Ic. Pl. 17: t.1727 (1888). Type: "Nieuweld [sic] Mountains near Fraserburg" Bolus 5493 (BL.!; G!; SAM!).

Neobakeria haemanthoides (Bak.) Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924).

Massonia pedunculata Bak. in Engl., Bot. Jahrb. 15, Beibl. 35: 8 (1892). Type: "Malmesbury prope Hopefield", Bachmann 2043 (K, holo., BOL, drawing!).

Massonia longipes Bak. in Fl. Cap. **6:** 411 (1897). Type: "near Danger Point, brought to the Cape Town garden by a visitor in 1884", *Bolus 5973* (K, holo.!). (This species is not known from Danger Point.).

Neobakeria namaquensis Schltr. in Notizbl. Bot. Gart., Berlin **9:** 150 (1924). Type: Zabies. Namaqualand, M. Schlechter 90 (BOL!; GRA!; PRE!).

Polyxena namaquensis (Schltr.) Krause in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, **15a**: 350 (1930).

Bulb globose or ovoid, (15–) 20–35 mm long, with whitish scales, surrounded by a few membranous brown scales. Leaves paired, oblong to oblong-ovate, acute, flat on the ground, spreading to erect-spreading, usually shiny, usually with several to many depressed veins, glabrous, sometimes with a minutely serrulate or crisped margin, (35–) 60–140 (–180) mm long, (13–) 20–60 (–100) mm broad. Inflorescence dense, capitate or somewhat elongate to 100 mm above the ground, rarely with up to 50 or more flowers, occasionally with a coma of sterile bracts above the fertile region. Lower bracts rather inconspicuous, ovate to obovate, (1–) 3–8 (–12) mm long. Pedicels very variable in length (1–) 12–18 (–29) mm long. Perianth white, sometimes tinged with reddish brown, or yellow to red,

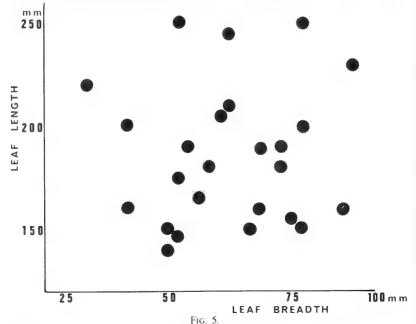


Diagram to illustrate variation in leaf measurements in *Massonia angustifolia* in a small population. Population area: Paternoster, behind hotel (3217; Vredenburg, Cape).

sometimes with the tube purple or purplish blue, often subchartaceous; tube usually longer than the segments, (4,5–) 7–12 (–17) mm long, 1,5–3 mm broad; segments erect, less often spreading, without a sigmoid fold towards the base, 7–11 (–15) mm long, 2–4 mm broad, ovate-oblong to linear. *Filaments* (8–) 10–16 (–18) mm long, free or connate to 1,5 mm, usually linear; anthers 1,25–2,75 mm long, yellow or reddish to almost black. *Style* 11–22 (–28) mm long. *Ovary* 4–8 mm long, ellipsoid. *Capsule* ellipsoid, with obtuse apex, 9 mm long.

Recorded from the inland dry parts of the Cape Province.

Occurs in dry, usually stony, areas, but also on sandy soils. Flowers, apparently never scented, are produced mainly in May and June.

M. Schlechter 90, from Zabies, Namaqualand, the type of Neobakeria namaquensis, has a tube "usque supra medium 6-fido" according to Schlechter (1924). But in a specimen in the Bolus Herbarium flowers examined had very short tubes (4,5–6 mm long) and longer segments (8,5–10 mm long). In all other respects this specimen matches other material placed in this species.

The most distinct species recognized by previous authors, but reduced to synonymy here, was *Polyxena haemanthoides*, characterized by a coma-like development of the sterile bracts above the inflorescence. The Bolus Herbarium sheet, however, comprises three specimens, in one of which the coma is rather well developed, while in another (as in the sheet in the South African Museum collection) there is very little or no evidence of this development.

Fig. 5 indicates variation in leaves in a population at Paternoster.

For illustration see Flower, Pl. S. Afr. 2: t.56 (1922).

SELECTED SPECIMENS

CAPE—2917 (Springbok): Zabies, M. Schlechter 90 (BOL, GRA, PRE).

- -2918 (Gamoep): 60 miles W. of Pofadder, Schlieben 9017 (PRE).
- —3022 (Carnarvon): Carnarvon, Liebenberg s.n. (STE).
- -3119 (Calvinia): 6 miles N. of Downes Station, Galpin 12890 (PRE).
- -3120 (Williston): Voelfontein, Sutherland, Hall 3242 (NBG).
- —3121 (Fraserburg): 6 miles NE. of Fraserburg, Acocks 14333 (PRE).
- -3123 (Victoria West): Victoria West, Whitlock 557 (PRE).
- —3217 (Vredenburg): Paternoster, Barker 10244 (NBG).
- —3220 (Sutherland): Fransplaas, Marloth 102556 (PRE).
- -3317 (Saldanha): Donkergat, Rourke 754 (NBG).
- 6. Massonia comata Burch. ex Bak. in J. Linn. Soc., Bot. 11: 392 (1871). Type: "Cap. b spei", *Burchell 2751* (K!).

Polyxena comata (Burch. ex Bak.) Bak. in Fl. Cap. 6: 419 (1897).

Neobakeria comata (Burch. ex Bak.) Schltr. in Notizbl. Bot. Gart., Berlin 9: 150 (1924).

Bulb globose to ovoid, 15-25 mm long, with white scales, surrounded by a few

membranous brown scales. *Leaves* usually paired, occasionally more numerous, lanceolate to ovate, acute, spreading, more or less flat on the ground, glabrous, usually with an undulate or crisped margin, sometimes with petiole-like sheath up to 70 mm long, 80–220 mm long, 15–60 mm broad. *Inflorescence* dense, capitate or somewhat elongate to 70 mm above the ground, with up to about 50 flowers. *Lower bracts* early deciduous, but probably up to 15 mm or more long. *Pedicels* 0–1 mm long. *Perianth* white, less often pink; tube cylindrical, 23–45 mm long. c. 1 mm broad; segments erect, without a sigmoid fold towards the base, 5–9 mm long, 1–1,5 mm broad, linear-oblong. *Filaments* 5–9 mm long, free, attached at the same level in the mouth of the perianth tube, linear; anthers about 1 mm long. *Style* 25–50 mm long. *Ovary* ellipsoid, 3–4 mm long, with c. 12 ovules per locule.

Recorded from the south-western Transvaal, Orange Free State and north-western Cape Province, although the records are rather scattered.

Occurs in heavy soils and reported from sandy alluvium. Flowers are scented, and are produced in winter.

The nearest affinity of this species is with M. angustifolia. Fig. 6 indicates the lengths of the perianth segments and of filaments in plants of these two species and indicates the justification for recognizing two species.

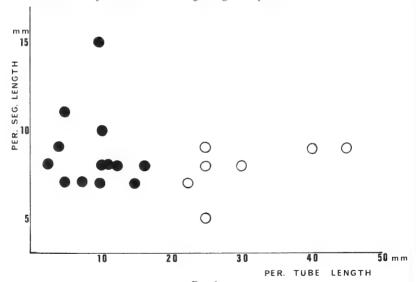


Fig. 6.

Diagram to illustrate the separation of Massonia angustifolia from M. comata on filament and perianth tube lengths. Solid dots represent plants with filaments over 9,5 mm long; open dots represent plants with filaments less than 9,5 mm long.

SELECTED SPECIMENS

TRANSVAAL—2725 (Bloemhof): Panfontein Game Reserve, *Louw 1828* (BOL, PRE).

ORANGE FREE STATE-2826 (Brandfort): Glen, Mostert 819 (PRE).

CAPE—2823 (Griekwastad): Griquatown, Wilman s.n. sub BOL 13933 (BOL).

- —2824 (Kimberley): 3 miles N. of Riverton, Leistner 1900 (PRE).
- —2923 (Douglas): St Clair, Herbert, Orpen 275 (BOL).
- -3024 (De Aar): De Aar, Friedlander s.n. (GRA).
- —3126 (Queenstown): 8 miles E. of Molteno, Stormsberg, Acocks 22097 (PRE).
- —3222 (Beaufort West): Beaufort West, Macarthy s.n. sub SAM 23080 (SAM).
- 7. Massonia jasminiflora Burch. ex Bak. in J. Linn. Soc., Bot. 11: 390 (1871). Type: "Cap. b spei", *Burchell B.7* (K, holo.!).

Massonia bowkeri Bak. in J. Linn. Soc., Bot. 11: 390 (1871). Type: "Orange Free State", Barber s.n. (TCD, holo.!).

Massonia greenii Bak. in Fl. Cap. **6:** 413 (1897). Type: "Griqualand West; stony places near Kimberley", MacOwan 2842 (K, holo.!; BOL, tracing!).

Bulb ovoid to ellipsoid, 10–20 mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, ovate to broadly oblong, acute, glabrous or rarely pustulate, occasionally with ciliate margins, flat on the ground, green, sometimes with red elongate markings, (25–) 30–60 mm long, 15–50 mm broad. Inflorescence capitate, generally with fewer than 15 flowers, but up to 35 recorded. Lower bracts ovate to obovate, 8–30 mm long, 6–20 mm broad, rarely minutely ciliate on the margins. Pedicels 3–5 mm long, Perianth white or pink; tube cylindrical, 8–20 mm long, 1,5–2,5 mm broad; segments with or without a sigmoid curve in the longitudinal axis towards the base, ascending or reflexed, 4–8 mm long, 1,5–2 mm broad. Filaments inserted in the throat of the perianth, 2–4,5 mm long, free or connate to 2 mm, deltoid, c. 15 mm broad at the base, white or pink; anthers green to blue, dark purple or black, c. 1–1,5 mm long. Style generally 5–7 mm long, sometimes minutely capitate. Ovary oblong-obovoid, shorter than the style.

Occurs in the eastern Cape, Lesotho, the Orange Free State, and northern Cape across the Orange River.

Recorded from limestone gravel and surface calcrete tufa, but occurring generally in open grassveld. The flowers are strongly scented and produced in May and June almost exclusively.

Leaves were taken from twelve flowering plants in a small population from the central Orange Free State to determine variation. These ranged in length from 25 to 42 mm and in breadth from 22 to 44 mm (30 miles SW. of Winburg, 2.7.72). See Fig. 7.

D. Collett, in a note on *Galpin 2612* (PRE), states that *M. bowkeri*, in which the filaments are free almost to their bases, is distinguishable from *M. jasminiflora*, in

which they are connate below for approximately half their length. "A second distinguishing feature is that in *M. bowkeri* the perianth segments are erect while in *M. jasminiftora* they are reflexed." Fig. 8 shows the lack of correlation found by the present author for these characters, indicating why the separation of these two species has not been upheld.

For illustration see Flower. Pl. S. Afr. 10: t.367 (1930).

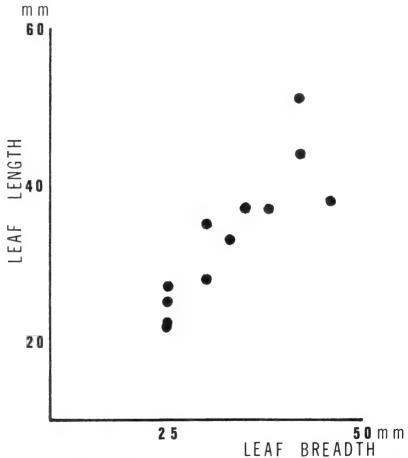


Fig. 7.

Diagram to illustrate variation in a small population of *Massonia jasminiflora*. Population area: "Vierkant" turning, north of Bloemfontein (30 miles SW. of Winburg) (2827; Senekal, Orange Free State).

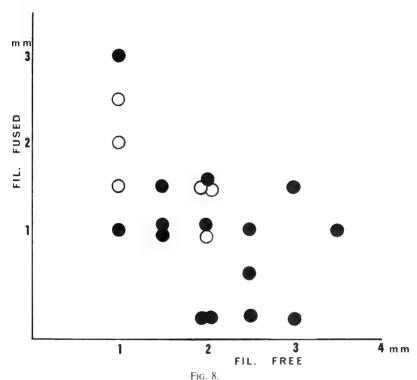


Diagram to illustrate variations in the lengths of free and fused parts of filaments of *Massonia jasminiflora*. Open dots indicate plants with reflexed perianth segments.

SELECTED SPECIMENS

TRANSVAAL—2725 (Bloemhof): Lopana, near Schweizer Reneke, *Bester s.n.* (PRE)

ORANGE FREE STATE—2727 (Kroonstad): Kroonstad, *Thurley s.n.* sub NH 11587 (NH).

- —2826 (Brandfort): Glen Agricultural College, Van der Berg 3948 (PRE).
- —2827 (Senekal): Marquard, Joubert s.n. sub NBG 1190/30 (BOL).
- -2925 (Jagersfontein): NE. of Fauresmith, Potter 2017 (PRE).
- —2926 (Bloemfontein): Bayswater, Potts s.n. sub BLFU 776 (PRE).
- -2927 (Maseru): Hobhouse, Thode A541 (NH, PRE).

LESOTHO-2828 (Bethlehem): Leribe, Dieterlen 724 (NH, SAM).

-2927 (Maseru): Roma, Ruch 1528 (PRE).

- CAPE—2723 (Kuruman): Kuruman, Hall s.n. sub NBG 71371 (NBG).
- —2824 (Kimberley): Kimberley, near Barkley West, Mogg 15122 (PRE).
- -3026 (Aliwal North): Ruigtefontein, Thode A1838 (PRE).
- -3027 (Lady Grey): Herschel, Phillips s.n. (NU).
- —3126 (Queenstown): Bowkers Kop, Galpin 1817 (BOL, PRE).
- —3226 (Fort Beaufort): Stockenstroom, Scully 54 (SAM).
- —3227 (Stutterheim): Cathcart, Cotterrell s.n. (BOL).

8. Massonia heterandra (Isaac) Jessop, comb. nov.

Neobakeria heterandra Isaac in Flower. Pl. S. Afr. **19:** t.729 (1939). Type: Villiersdorp, *Stokoe s.n.* sub BOL 22309 (BOL, holo.!; PRE!; SAM sub SAM 52826!).

Bulb ovoid, (12-) 15-20 (-25) mm long, with whitish scales, surrounded by a few firm membranous brown scales. Leaves paired, glabrous, papillate or more often pustulate (sometimes the pustules muricate), often with ciliate margins, green with or without purple spots or streaks, erect-spreading to spreading, ovate to obovate or almost orbicular, with acute apex, 14-30 (-40) mm long, 7-18 mm broad; petiole-like base 0-30 mm long. Inflorescence capitate to shortly corymbose, with usually 2-6 flowers. Lower bracts oblanceolate to obovate, with acute apex, 12-20 mm long, (2,5-) 3-5 mm broad. Pedicels 5-12 mm long. Perianth pink or white; tube 6-14 (-17) mm long, 0,5-2 mm broad, linear; segments linear-oblong, 4-7 mm long, 0,5-2 mm broad, erect to spreading. Filaments inserted at mouth of perianth tube, almost free or connate to 1 mm, usually of two different lengths in one flower but not always with all members of each whorl of the same length as one another, 2,5-7 (-8) mm long; anthers dark purple-black, 1–1,5 mm long. Style c. 11–12 mm long, cylindrical. Ovary ellipsoid, green, 3-4 mm long. Capsule obovoid, shortly acute at the apex, c. 6-7 mm long; seeds c. 1–1,5 mm diameter.

Restricted to the south-western Cape. Inhabits high altitudes in sand and in rock crevices. Flowers mainly in April and May.

For illustration see Flower. Pl. S. Afr. 19: t.729 (1939).

SELECTED SPECIMENS

CAPE—3219 (Wuppertal): Cedarberg Tafelberg, Esterhuysen 21370 (BOL, NBG, PRE); Middelberg, Esterhuysen 7865 (BOL); Scorpionsberg, Esterhuysen 12219 (BOL).

—3319 (Worcester); Hansiesberg, *Esterhuysen 25722* (BOL); Louws Hoek, *Stokoe s.n.* sub BOL 22309 (BOL, PRE); Kaaimans Peak, *Esterhuysen 32132* (BOL); Wemmershoek Tafelberg, *Stokoe s.n.* (BOL); Villiersdorp, *Stokoe s.n.* sub SAM 52826 (SAM).

Polyxena Kunth Enum. Pl. 4: 294 (1843).

Bulbs small, with a few outer brown membranous scales, with white more or less tubular inner scales and one inner membranous translucent tubular scale

ensheathing the base of the aerial parts. Leaves 2–6, usually erect, less often spreading, linear to broadly lanceolate, glabrous. *Inflorescence* racemose, sometimes corymbose, with small inconspicuous bracts subtending the pedicels. *Flowers* actinomorphic, pedicellate, usually pink or white. *Perianth* fused to form a long tube, dehiscing at the base leaving a conspicuous annular scar at the base of the young fruit; the perianth adhering to the apex of the developing fruit; free segments more or less oblong, never with a sigmoid folding towards the base, often minutely papillate at the apex. *Stamens* often of two different lengths and usually attached to the perianth tube at two different levels; filaments always distinctly free of one another, sublinear, bearing dorsifixed oblong to linear anthers. *Ovary* sessile, ellipsoid; each carpel containing several ovules, usually much shorter than the perianth tube. *Style* sublinear, usually slightly longer than the stamens; stigma subcapitate to undifferentiated. *Fruit* a loculicidal capsule containing numerous black subglobose seeds about 1–2 mm diameter.

Type: P. pygmaea (Jacq.) Kunth (= P. ensifolia (Thunb.) Schonl.)

The very regular arrangement of bulb scales, incorporating the lamina-less bract-like membranous ensheathing scale, and the biseriate stamens are characteristic. The absence of spathe-like bracts and of the sigmoid folding of the perianth segments also serves to separate it from the majority of *Massonia* specimens.

Species concepts in Polyxena. Baker (1896–7) recognized four species in his concept of *Polyxena* subgenus *Eupolyxena* (subgenus *Astemma* is here placed in *Massonia*) and a further one has since been described. He also recognized two species of *Hyacinthus* in the south-western Cape. A third species has since been described.

Characters used by previous authors to distinguish between these eight species have been: flower colour, the comparative lengths of perianth segments and tubes, the degree of separation of the insertion of the staminal whorls and the type of inflorescence.

However, these characters have generally been found to grade into one another and not to provide suitable characters for distinguishing species. Most species, previously placed in subgenus *Eupolyxena*, are treated by the present author as synonymous, while all species previously placed in *Hyacinthus* (Cape species) are treated as a second species. Two species treated by Baker (1897) in *Eupolyxena* are excluded – *P. bakeri* is a synonym for *Massonia echinata* and *P. uniflora* (= *M. uniflora*) is a *nomen dubium*.

KEY TO THE SPECIES OF POLYXENA

1 Leaves rarely less than 8 mm broad; perianth tube 7 mm or more long1. ensifolia 1a Leaves 1–3 mm broad; perianth tube 6 mm or less long2. corymbosa

1. **Polyxena ensifolia** (Thunb.) Schonl. in Trans. Roy. Soc. S. Afr. **1:** 443 (1910). *Mauhlia ensifolia* Thunb., Prodr. 60, t.1 (1794). Type: Cape, without precise

locality, Thunberg s.n. (UPS, holo., microfiche!).

Agapanthus ensifolius (Thunb.) Willd., Sp. Plant. 2: 48 (1799).

Massonia ensifolia (Thunb.) Ker-Gawl. in Curtis's bot. Mag. 16: t.554 (1802). Polyanthes pygmaea Jacq., Icones 2 (16): 15, t.380 (1795). Type: Cape, without

precise locality or collector, Jacq., Icones 2 (16): 1.380 (1795).

Polyxena pygmaea (Jacq.) Kunth, Enum. Pl. 4: 294 (1843).

Massonia violacea Andr. in Bot. Rep.: t.46 (1797). Type: Cape, without precise locality or collector, from the collection of G. Hibbert, Andr. in Bot. Rep. t.46 (1797).

Hyacinthus bifolius Bout. in Anal. Cienc. Nat. 5: 14, t.41, fig. 1 (1802). Type: Cape, without precise locality or collector, from the Royal Botanic Garden, Madrid, Bout. in Anal. Cienc. Nat. 5: t.41, fig. 1 (1802).

Massonia odorata Hook.f. in Curtis's bot. Mag. 97: t.5891 (1871). Type: Cape, Colesberg district, Arnot s.n. (K, holo.!; BOL, drawing!).

Polyxena odorata (Hook.f.) Nicholson, Dict. Gard. 3: 196 (1886), comb. invalid.

Polyxena odorata (Hook.f.) Bak. in Fl. Cap. 6: 420 (1897).

Polyxena maughanii Barker in Flower. Pl. S. Afr. 11: t.420 (1931). Type: Nieuwoudtville, Maughan Brown & Bolus s.n. sub BOL 19613 (BOL, holo.!).

Bulb depressed globose to ovoid, with white fleshy scales and a few outer brown membranous scales, (8-) 10-20 (-28) mm long. Leaves paired, broadly oblanceolate or lanceolate to linear, acute, often with a long tapering apex, often with conspicuously depressed veins, glabrous, sometimes with ciliate or minutely fimbriate margins, occasionally red along the margin, flat on the ground or more frequently more or less erect, (20-) 30-120 (-170) mm long, (3-) 8-25 (-35) mm broad, sometimes with a petiole-like base to 110 mm long. Inflorescence more or less corymbose and partly immersed in the leaves, with (1-) 10-20 (-35) flowers. Bracts inconspicuous, usually ovate, acute or acuminate, 1-5 mm long. Pedicels (1-) 5-12 (-16) mm long. Perianth white or pink to mauve; tube sublinear, but expanding slightly towards the mouth, (7-) 10-20 (-25) mm long, c. 1 mm broad; segments oblong (4-) 5-10 mm long, 1-2 mm broad, ascending or spreading. Filaments linear, inserted in two more or less distinct rows on the segments and/or the tube, 2-6 mm long, frequently the whorl inserted higher on the perianth is up to 2 mm longer than the lower; anthers yellow to almost black, 1-1,5 mm long. Style sublinear, 10-18 mm long; stigma minutely capitate or undifferentiated. Ovary ellipsoid, 3-4 mm long. Capsule ovoid to ellipsoid, 4,5-9 mm long, 4-6 mm broad.

Widespread in the Cape Province from the coast to the interior, but not from the extreme north or east.

Recorded from clay flats, shaly flats, rock crevices and sandy soils in the shade

and in the open. Localities fall within fynbos, grassveld and semi-desert vegetation types. Flowers are often strongly scented and produced from April to June.

Schlechter 10549 from Zeekoevley (PRE) and Leipoldt 4115 from Kransvlei (PRE) are unusual in having 3–6 leaves, but these are not otherwise atypical.

Despite the several species recognized by previous authors, this is in fact a rather homogeneous species, specimens differing in quantitative measurements as indicated in the description, but with no qualitative variability.

For illustration see Flower. Pl. S. Afr. **4**: t.129 (1924) and Flower. Pl. S. Afr. **11**: t.420 (1931).

SELECTED SPECIMENS

- CAPE—2917 (Springbok): O'Okiep, Good s.n. sub NBG 71406 (NBG).
- -3017 (Hondeklipbaai): 20 miles NW. of Garies, Salter 6676 (BOL).
- —3018 (Kamiesberg): near Leliefontein, Van Heerde s.n. sub NBG 84208 (NBG).
- -3022 (Carnaryon): Carnaryon, Pillans s.n. sub NBG 3742/14 (BOL).
- -3024 (De Aar); De Aar, Friedlander s.n. (GRA).
- -3119 (Calvinia): Nieuwoudtville, Leipoldt 4209 (BOL).
- -3120 (Williston): Voelfontein, Hall 223 (NBG, PRE).
- -3123 (Victoria West): Richmond, Bolus s.n. (BOL).
- -3124 (Hanover): Hanover, Acocks 13759 (PRE).
- —3218 (Clanwilliam): 6,6 miles from St Helena Bay to Velddrift, *Thompson 288* (PRE).
- -3219 (Wuppertal): Fransplaas, Marloth 9822 (PRE).
- -3220 (Sutherland): below Verlaten Kloof, Acocks 18187 (PRE).
- —3222 (Beaufort West): Beaufort West, Macarthy s.n. sub SAM 23077 (SAM).
- -3225 (Somerset East): Cradock, Lang s.n. sub Marloth 6851 (PRE).
- —3319 (Worcester): between Ceres and Karoopoort, *Leipoldt s.n.* sub BOL 20092 (BOL).
- -3320 (Montagu): Constable, Drège 2187 (HAL, L, SAM).
- -3322 (Oudtshoorn): Cango, Compton 10734 (NBG).
- -3323 (Willowmore): near Avontuur, Fourcade 1314 (GRA, BOL).
- —3324 (Steytlerville): 18,5 miles N. of Humansdorp, Acocks 13720 (PRE).
- -3325 (Port Elizabeth): Uitenhage, Schlechter 2600 (GRA, PRE).
- -3326 (Grahamstown): Alexandria, Galpin 10861 (PRE).
- -3419 (Caledon): near Elim, Schlechter 10471 (GRA, L, PRE).
- -3420 (Bredasdorp): De Hoop, Barker 8742 (NBG).
- —3421 (Riversdale): Albertinia commonage, Muir 915 (PRE, SAM).

2. Polyxena corymbosa (L.) Jessop, comb. nov.

Hyacinthus corymbosus L., Mantissa Altera: 223 (1771). Type: "Cap. b. spei", Koenig s.n. not located. The specimen in LINN was not, according to Savage (1945), annotated by Linnaeus, was not identified as originating from Koenig and

cannot be accepted as the type. However, as evidenced by the comparatively large number of old records, this appears formerly to have been very common around Cape Town, and the description is sufficiently full to make it certain that the name is correctly applied.

Massonia corymbosa (L.) Ker-Gawl. in Curtis's bot. Mag. 25: t.991 (1807). Scilla corymbosa (L.) Ker-Gawl. in Curtis's bot. Mag. 36: t.1468 (1812).

Periboea corymbosa (L.) Kunth, Enum. Pl. 4: 293 (1843).

Periboea gawleri Kunth, Enum. Pl. 4: 293 (1843), nom. nov. for Scilla brevifolia sensu Ker-Gawl. in Curtis's bot. Mag. 36: t.1468 (1812), non Hyacinthus brevifolius Thunb. Type: Ker-Gawl. in Curtis's bot. Mag. 36: t.1468 (1812). Hyacinthus gawleri (Kunth) Bak. in Fl. Cap. 6: 472 (1897).

Hyacinthus paucifolius Barker in Jl S. Afr. Bot. 7: 198–200 (1941). Type: Vredenburg, Mathews s.n. sub NBG 689/30 (NBG, holo.!; PRE!).

Bulb globose to ovoid, with white fleshy scales and usually a few outer brown membranous scales, 7–15 mm long. Leaves 2–6, linear, slightly channelled above, erect to spreading, but never flat on the ground, glabrous, 30–70 (–120) mm long, 1–3 mm broad. Inflorescence racemose, sometimes corymbose, 20–75 (–90) mm long, with 1–8 flowers. Bracts inconspicuous, 0,5–1 mm long. Pedicels usually 3–5 mm long, up to 8 mm in fruit. Perianth pink, sometimes with a darker median stripe on the dorsal surface; tube linear, expanding to the mouth, 3,5–6 mm long, 1,5–2 mm broad; segments oblong, 6–9 mm long, 1–2,5 mm broad, erect-spreading. Filaments linear, inserted at two distinctly different levels in the tube, 1–5 mm long; anthers yellow, c. 1 mm long. Style minutely capitate, sublinear, broadest towards the base, 1–7 mm long. Ovary oblong or globose, often rather deeply 3-lobe, 1,5–3,5 mm long. Capsule 3-lobed, 3–4 mm long; seeds subglobose, 1–2 mm diameter.

Restricted to the south-western Cape Province, from Gordon's Bay to Clanwilliam.

Recorded from sandy soil, and less often from either gravelly soils or rock crevices. Flowers in April and May, although occasionally recorded in spring as well.

While *Hyacinthus paucifolius* is certainly atypical in the aspects mentioned by Barker (1941), especially the very short style and filaments, in the opinion of the present author it only represents an extreme in the range now recorded for *P. corymbosus* as defined here.

For illustration see Jl S. Afr. Bot. 7: 199 (1941) and Kidd, M. M. (1950) Wild flowers of the Cape Peninsula, pl. 33, fig. 9.

SELECTED SPECIMENS

CAPE—3217 (Vredenburg): Paternoster, Steytler s.n. sub NBG 549/31 (BOL); Witklip Farm, Barker 10173 (NBG).

—3218 (Clanwilliam): Warmbaths, Edwards s.n. sub BOL 14437 (BOL).

- —3318 (Cape Town): between Malmesbury and Hopefield at Oude Post, *Salter* 4409 (BOL); Greenpoint Race Course, *Zeyher 1715* (BOL); Camps Bay, *Rehmann 1608* (Z); Stellenbosch, *Duthie 417* (BOL).
- -3319 (Worcester): New Kloof, near Tulbagh, Bolus 5363 (BOL).
- —3418 (Simonstown): Strand to Gordon's Bay, Parker 4320 (BOL, NBG).

Daubenya Lindl. Bot. Reg. 21: t.1813 (1835).

Bulb subglobose, (16–) 20–35 mm long, with brown membranous outer scales. Leaves paired, glabrous, flat on the ground, elliptic to ovate, obtuse, often brownish towards the apex, (50-) 80-140 mm long, 35-75 mm broad. Inflorescence largely immersed in the leaves, capitate, with about 10 flowers. Lower bracts oblong, 15-30 mm long, 5-15 mm broad, conspicuous. Pedicels 5-6 mm long. Perianth red, orange or yellow; outer flowers strongly zygomorphic, fused to form a tube 35-40 mm long on the side of the larger lip (abaxial), 20-30 mm long on the side of the smaller lip (adaxial), c. 4 mm in diameter; the 3 shorter (adaxial) segments obovate, 7–10 mm long, 2–3 mm broad; the 3 larger (abaxial) segments obovate, 19-40 mm long, 10-20 mm broad; inner flowers actinomorphic; tube 20-25 mm long; segments 3-6 mm long. Filaments subulate, attached to the mouth of the perianth, not connate; those on adaxial lip of outer flowers 5–10 mm long; those on abaxial lip of outer flowers 3–7 mm long; anthers 2–3 mm long, yellow. Style c. 25 mm long. Ovarv ellipsoid, 7-8 mm long, 3-lobed towards the base. Capsule ovoid, not winged, 12-20 mm long; seeds globose, 2 mm diameter

Type: D. aurea Lindl.

Baker recognized three species: *D. fulva* with a longer peduncle and known only from a plant grown in England, and *D. aurea* and *D. coccinea* distinguished in the key on flower colour. Both Marloth (Flower. Pl. S. Afr. 2: t.77; 1922) and Hall (1970) who examined populations in the field concluded that only a single species should be recognized. Examination of the limited herbarium material has confirmed this opinion.

Daubenya aurea Lindl. in Bot. Reg. **21:** t.1813 (1835). Type: "Cape of Good Hope", without precise locality or collector, cultivated by Messrs Young of Epsom, Lindl. in Bot. Reg. **21:** t.1813 (1835).

Daubenya fulva Lindl. in Bot. Reg. 25: t.53 (1839). Type: "received from the Cape of Good Hope, with other bulbs, but was believed to have been collected somewhere on the East Coast of Africa or in Madagascar", without particulars (CGE!). There is no adequate reason to accept that the type did not come from the Cape.

Daubenya coccinea Harv. ex Bak. in J. Linn. Soc., Bot. 11: 395 (1871). Type: "Cap. b. spei", Harvey s.n. (TCD, holo.!).

Collected from a small area of the south-western Karoo.

Field records indicate a preference for stony, clay soils. Flowers have an unpleasant scent and have been recorded in August and September.

SELECTED SPECIMENS

CAPE—3120 (Williston): near Voelfontein Farm, *Hall 3240* (NBG); 40 miles NW. of Sutherland on left of Sutherland–Middelpos road, *Hall 3269* (NBG, PRE).

—3219 (Wuppertal): Fransplaas, 40 miles W. of Sutherland, *Marloth 10415* (BOL, PRE, STE).

—3220 (Sutherland): Modderfontein, Meiring s.n. sub NBG 2775/15 (BOL).

Androsiphon Schltr. in Notizbl. Bot. Gart., Berlin 9: 148 (1924).

Bulbs ovoid, 10–20 (–25) mm long. Leaves paired, spreading, glabrous, more or less elliptic, 80–150 mm long, 30–60 (–100) mm broad, dark green spotted with darker green, sometimes with minutely fimbriate margins. Inflorescence capitate. Lower bracts lanceolate, acute, 25–30 mm long, 2–3 mm broad. Pedicels 15–30 mm long. Flowers golden yellow, actinomorphic, pedicillate. Perianth tube 6–11 mm long, 3–4,5 mm diameter; segments erect or erect-spreading, linear-oblong, 11–13 mm long, 2,5–3 mm broad. Filaments connate to form a cylindrical tube c. 11 mm long, which is attached to the mouth of the perianth tube; free portion of filaments erect-spreading, subulate, 9–13 mm long, sometimes of two lengths – as much as 4 mm difference in a single flower; disc formed at top of filament tube, pierced by the style; anthers 2–3 mm long. Style subcapitate, 20–26 mm long. Ovary ellipsoid, 7–9 mm long, with c. 8–15 ovules per locule. Capsule narrowly obovoid, subtruncate apically, recorded in the type description as leathery but appearing membranous in the material; dehiscence loculicidal; seeds globose, 3 mm diameter.

Type: A. capense Schltr.

Monotypic.

Androsiphon capense Schltr. in Notizbl. Bot. Gart., Berlin 9: 147–149 (1924). Type: Onder Bokkeveld, Oorlogskloof in collibus, *Schlechter 10969* (BOL!; G!; GRA!; PRE!).

Restricted to a small area in the western karoo.

Flowers are produced in winter - recorded in June, August and September.

For illustration of flower see Jl S. Afr. Bot. 2: 21 (1936).

SELECTED SPECIMENS

CAPE—3119 (Calvinia): Oorlogskloof in hills, *Schlechter 10969* (BOL, G, GRA, PRE); Nieuwoudtville, *Leipoldt 796* (BOL); Plaatberg Farm, SW. of Calvinia, *Acocks 18606* (PRE).

Amphisiphon Barker Jl S. Afr. Bot. 2: 19-23 (1936).

Bulbs globose, with dark brown outer scales, 25–35 mm long. Leaves paired or rarely 3, spreading or erect-spreading, ovate, 45–50 (–95) mm long, 15–20 (–42)

mm broad, dark green, glabrous. *Inflorescence* hardly exserted beyond leaves, capitate. *Bracts* similar, inconspicuous, lanceolate, *c*. 10 mm long. *Pedicels c*. 3 mm long. *Perianth* greenish yellow above, white below, fused to form a cylindrical tube 10–20 mm long, with yellow erect oblong free segments (1,5–) 3 mm long, 1,5 mm broad. *Filaments* connate to form a tube 11–15 mm long, attached to the perianth tube just below the middle; free portion of filaments erect-spreading, arcuate, yellow, 9–10 mm long; anthers 1,5–2 mm long. *Style* yellow, subulate, with the stigma undifferentiated, 20–30 mm long. *Ovary* narrowly ovoid, 5–8 mm long, with many ovules. *Capsule* "membranous, ovate, obtusely angled, laterally compressed parallel with the peduncle, 12 mm diam.; style persistent; dehiscence septicidal from the base; seeds 2,5 mm long" (Barker, 1936).

Type: A. stylosa Barker. Monotypic.

Amphisiphon stylosa Barker in J1 S. Afr. Bot. **2:** 19–23 (1936). Type: 3 miles N. of Nieuwoudtville, *Salter* 4552 (BOL, holo.!).

Known only from a single collection. Flowers are scented and produced in June, although a cultivated plant flowered in May.

For illustration see Barker (1936).

ONLY SPECIMEN KNOWN:

CAPE-3119 (Calvinia): 3 miles N. of Nieuwoudtville, Salter 4552 (BOL).

Whiteheadia Harv. Gen. S. Afr. Pl., ed. 2: 396 (1868).

Bulbs subglobose, 20–30 mm long. Leaves paired, glabrous, flat on the ground, elliptic, subacute, sometimes with the veins conspicuously immersed, (80–) 100–200 (–400) mm long, 60–150 (–250) mm broad. Inflorescence a raceme, 55–150 mm high, rarely 350 in fruit, with up to 50 (or less often more) flowers. Bracts more or less similar, green, ovate-acuminate, 25–40 mm long, 12–20 mm broad. Pedicels 3–4 mm long. Perianth whitish or green with white margin, fleshy; tube 4–7 mm long; segments 6–7 mm long, deltoid to oblong. Filaments with a connate tube 2 mm long; free parts 6–7 mm long; anthers 2,5–3,5 mm long. Ovary ovoid, 4 mm long. Style 1–3 mm long; stigma not differentiated. Capsule surrounded at first by persistent (not marcescent) perianth, with approximately 12 seeds per locule, strongly 3-winged, sub-truncate apically, with a persistent style; the body of the capsule (excluding wings) ovoid, 15–25 mm long.

Type: W. latifolia Harv. (= W. bifolia (Jacq.) Bak.). Monotypic.

Whiteheadia bifolia (Jacq.) Bak. in J. Linn. Soc., Bot. 13: 226 (1873).

Eucomis bifolia Jacq., Collect. 4: 215 (1791), Icones 2 (16): 21, t.449 (1795). Type: Cape of Good Hope, without precise locality or collector, Jacq., Icones 2 (16): t.449 (1795). This illustration may not be regarded as part of the original diagnosis but as it is based on material common to the type description it is justified to treat this, in the absence of an actual specimen, as the type.

Basilaea bifolia (Jacq.) Poir., Encyc. Suppl. 1: 591 (1811).

Melanthium massoniaefolium Andr., Bot. Rep. 6: t.368 (1804). Type: "in the Hibbertian collection", Andr. Bot. Rep. 6: t.368 (1804).

Whiteheadia latifolia Harv., Gen. S. Afr. Pl., ed. 2: 396 (1868). Type: Modderfontein, Namaqualand, Rev. Henry Whitehead s.n. (TCD, holo.!).

Recorded from the western dry areas of the Cape and the extreme south of South West Africa.

Occurs in rocky places; in both damp and dry situations. Flowers in winter.

For illustration see Flower. Pl. Afr. **37:** t.1450 (1965), where Obermeyer described the leaves as "having a characteristic succulence and fragility; the lamina breaking readily" and "water dripping onto it will pierce it".

SELECTED SPECIMENS

SOUTH WEST AFRICA—2828 (Warmbad): Farm Sperlingspütz, Giess, Volk & Bleissner 6972 (PRE).

CAPE—2917 (Springbok): Steinkopf, *Marloth 6766* (PRE, STE); Ratelpoort, below Springbok and Steinkopf, *Hardy 542* (PRE); near Klipfontein, *Bolus 6565* (BOL); Mesklip, *Lewis 1396* (SAM).

—3017 (Hondeklipbaai): Kamieskroon, *Thorne s.n.* sub SAM 48856 (SAM); Brakdam, *Leighton 1373* (BOL); 11 miles WSW. of Garies, *Acocks 14926* (PRE).

—3018 (Kamiesberg): Studer's Pass, Kamiesberg, *Thompson 425* (PRE, STE); Giftberg, *Compton 20842* (NBG).

—3119 (Calvinia): near Nieuwoudtville, *Marloth 8343* (PRE); top of Botterkloof, *Esterhuysen 3871* (BOL).

—3218 (Clanwilliam): Kransvleibergen, Leipoldt 322 (SAM).

-3219 (Wuppertal): Pakhuis, Esterhuysen 3157 (BOL).

Nomina Dubia

Massonia breviscapa Lehm., Delect. Sem. Hort. Hamb. 8 (1838), type description not located.

Massonia cordata Jacq., Hort. Schoenbr. 4: 30, t.459 (1804). Type: Jacq., Hort. Schoenbr. 4: t.459 (1804), not identifiable.

Massonia coronata Jacq., Hort. Schoenbr. 4: 30, t.460 (1804). Type: Jacq., Hort. Schoenbr. 4: t.460 (1804), not identifiable.

Massonia laeta Masson ex Bak. in J. Bot., Lond. 1886: 336 (1886). Type: "Summit of the Kamiesberg", Masson s.n. (drawing in BM, BOL, copy!), not identifiable.

Massonia longifolia Jacq., Hort. Schoenbr. 4: 29, t.457 (1804). Type: Jacq., Hort. Schoenbr. 4: t.457 (1804), not identifiable.

Massonia lanceaefolia Jacq., Hort. Schoenbr. **4:** 29, t.456 (1804). Type: Jacq., Hort. Schoenbr. **4:** t.456 (1804), not identifiable.

Massonia nervosa Hornem., Hort. Hafn., Suppl. 39 (1819). Type: "Cap. b. spei", without collector, not located and description inadequate.

Massonia nodicarpa Gaertn.f., Fruct. 3: 13, t.182 (1805). Type: Gaertn.f., Fruct. 3: t.182 (1805), not identifiable.

Massonia pauciflora Ait.f., Hort. Kew., ed. 2, 2: 210 (1811). Type: "Cape of Good Hope", Masson s.n., not located and description inadequate.

Massonia uniflora Banks ex Bak. in J. Linn. Soc., Bot. 11: 393 (1871). Type: "Cap. b. spei (v.s. in Herb. Mus. Brit.)", not located and description inadequate. *Polyxena uniflora* (Banks ex Bak.) Bak. in Fl. Cap. 6: 421 (1897).

ACKNOWLEDGEMENTS

The author is greatly indebted to the staff of the National Botanic Gardens, Kirstenbosch (both of the Gardens and of the Compton Herbarium) for facilities and material put at his disposal. Miss W. F. Barker's knowledge of the western Cape Liliaceae has been of particular value.

Mrs A. A. Mauve, Botanical Research Institute, Pretoria, has also been a source of a great deal of encouragement and advice.

Col. R. D. A. Bayliss has very kindly made a number of collections of living material for this work.

The use of the Botanical Research Unit Grahamstown, and Albany Museum facilities is gratefully acknowledged.

Travelling expenses in connection with visits to herbaria and for field-work have been subsidized by the C.S.I.R.

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A PRELIMINARY REVIEW OF THE PROMINENTLY PAPILLOSE HUERNIA SPECIES (ASCLEPIADACEAE)

L. C. LEACH*

ABSTRACT

19 species of *Huernia*, characterised by their prominently papillose corollas, are reviewed and their apparent affinities, diagnostic characters, variation and distribution discussed in detail; attention is also given to synonymy and nomenclatural matters. Maps showing the known distribution of the species are provided, as well as an artificial key to the taxa now recognised. One new variety is described and *H. nigeriana* is re-instated at specific level.

UITTREKSEL

'N VOORLOPIGE HERSIENING VAN DIE PROMINENTE PAPILOORTREKTE HUERNIA SOORTE (ASCLEPIADACEAE)

Negentien *Huernia* soorte, gekenmerk deur 'n papiloortrekte blomkroon, word hersien en hulle skynbare verwantskappe, onderskeidende kenmerke, variasie en verspreiding word in besonderhede beskryf; aandag word ook aan die sinonieme en nomenklatoriese sake gegee. Kaarte wat die bekende verspreiding van die soort toon, word aangegee, asook 'n kunsmatige sleutel tot die taksa wat nou erken word. Een nuwe variëteit word beskryf en *H. nigeriana* word weer as 'n soort erken.

INTRODUCTION

The species of *Huernia* distinguished by prominently papillose corollas appear to form a related group, although it seems possible that several phyletic lines may be involved, with convergence accounting for some of the similarities. On the other hand there seems a distinct possibility that there may once have been a more continuous distribution pattern. Evidence of this may well exist today but remain undiscovered, as the area lying between the northern and central groupings has been far from intensively botanised; furthermore, examples from other groups of the genus are by no means absent from this area. Among these are *H. aspera* N.E.Br., now known from as far south as Liwonde in Malawi, and *H. verekeri* Stent, until recently thought to be of relatively restricted distribution, from Zambia and Malawi as well as westward almost to the Atlantic coast, while very recently the rare *H. leachii* Lavr. from central Moçambique has been found near Lake Malawi.

Among the distinguishable subdivisions of the group, the *H. hystrix-stapelioides-volkartii* complex appears to form one series while the northerly based

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species (including *H. nigeriana*) may represent another. The possible evolutionary background of the geographically more centrally situated species, including *H. kirkii*, *H. hislopii*, *H. levyi*, etc., appears to be rather more obscure, although there seems little doubt that the species involved are quite closely related.

The decision, based on morphological characters, to retain *H. volkartii* at specific level and to reinstate *H. nigeriana* is supported by the available cytological evidence, as well as providing a phytogeographically somewhat more acceptable solution for the affinities involved. Both varieties of *H. volkartii* are tetraploid while *H. nigeriana* is diploid, as are both *H. hystrix* and *H. stapelioides*.

The southernmost group, with quite different, multi-angular stems (*H. kenne-dyana*, *H. longii*, *H. pillansii* and the possibly hybrid *H. distincta*), appears to belong in a rather more divergent, albeit closely related, line of development.

In this article reference is made to the corona and its inner and outer lobes rather than to the inner and outer coronas, as the implication that there are two separate coronas is considered to be most misleading. Similarly, it is not always clear, in descriptions, exactly what is meant by the length of the inner lobes. Where given in the following text this is as indicated in the accompanying sketch, which also shows a typically "huernia" arrangement of the anther wings and nectarial orifice (or stigmatic cavity) with a small tubercle at its base. Although the function of the tubercle (usually present, although varying considerably in size and prominence, in *Huernia* but apparently absent from *Duvalia*) is obscure there does seem to be a measure of correlation between the length of the caudicles connecting the pollinia to the translator (generally short in Huernia and long in Duvalia) and the distance between the base of the anther wings and the nectarial orifice. This seems possibly to indicate that the orifice and cavity may provide an alternative path for the pollen-tubes additional to that described by the late Dr. Reese (1973), and that the term "stigmatic cavity" may thus be correct in its implication. This orifice is herein referred to as "nectarial" as it appears to be, in at least some species, the source of the "nectar" (attractant would perhaps be a more suitable term) which appears to be the origin of the mostly foetid odours emitted by most members of the tribe. However, whatever the precise function of this cavity (and in Huernia its attendant tubercle), it seems that much remains to be learnt concerning the pollination of these interesting plants.

Characters more or less common to the group include:

Stems: glabrous, estipulate, variably tuberculate-dentate.

Inflorescence: flowers developed singly, successively, usually from near the base of the stems.

Bracts: subulate.

Corolla: limb and lobes and within the mouth of the tube, more or less densely covered with prominent fleshy papillae, which are longest around the mouth of the

tube opposite the intermediate lobes and progressively reduced in size towards the apex and margins of the lobes.

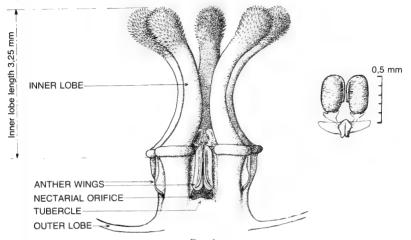


Fig. 1.

Characteristic "huernia" corona (*H. longituba* subsp. *longituba*, N of Kanye, Botswana, *Leach et al.* 12469).

Corona: more or less as illustrated above, sessile, with the outer lobes closely adpressed to the base of the tube, mostly so variably shaped as to be diagnostically valueless; inner lobes are of two forms, both enlarged often transversely gibbous at the base, and (1) clavate or appendaged at the apex and (2) those usually referred to as "subulate" (i.e. tapering to a small, obtuse apex); the former, although very variable, are usually identifiable with a given taxon.

Pollinia: more or less elliptic or oblong-elliptic, attached to the translator by short translucent caudicles which are often laterally much expanded just below the point of attachment to the pollinium. The shape of the pollinia and the length of the caudicles appear to be more or less constant for the genus. Although there seems a slight possibility that pollinium size may be to some extent of taxonomic significance it seems more probable that it may prove merely to be a factor of flower size.

Other characters which are more diagnostic are dealt with under the individual taxa.

A list of the species discussed:

1. H. hystrix	4. H. volkartii
2. H. stapelioides	5. H. nigeriana
3. H. loesenerana	6. H. lodarensis

7. H. erinacea	14. H. kirkii
8. H. recondita	15. H. longituba
9. H. boleana	16. H. kennedyana
10. H. whitesloaneana	17. H. pillansii
11. H. occulta	18. H. longii
12. H. hislopii	19. H. distincta
13. H. levvi	

The line drawings accompanying the specific descriptions depict characteristic inner corona-lobes and examples of the largest papillae from the throat and around the mouth of the corolla tube (mostly in both front and side view); these are generally specifically diagnostic and may be used pictorially to "key-out" specimens.

Identification of the taxa is often possible from examination of only one or other of these illustrated features, while their various combinations are almost always conclusively diagnostic despite the extent of their variability. In the few instances where doubt may arise it will be found that the stem and/or corolla characters provide adequate additional evidence of identity, e.g. *H. erinacea*, vs. *H. lodarensis* or the subspecies of *H. pillansii*.

The species dealt with are on the whole very well differentiated and it is considered that identification of live or "spirit" material should present no problem; however, as some characters are difficult to interpret in dry specimens, the correct placing of these is often more difficult. With this in mind, supplementary and confirmatory characters have been included wherever possible in the following key.

AN ARTIFICIAL KEY TO THE TAXA

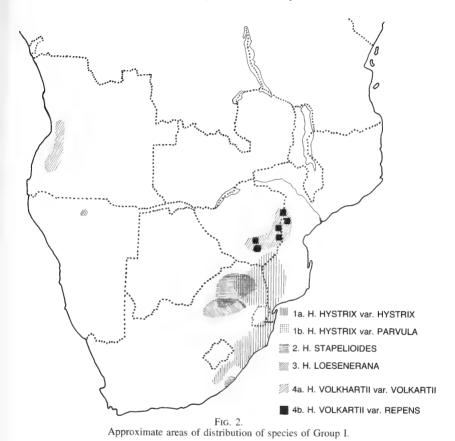
1.	Inner corona-lobes clavate, ventricose-clavate, truncate-clavate, sharply expanded and somewhat foot-like at the apex, or rarely stoutly obtuse and very slightly subclavate
	Inner corona-lobes subulate, obtuse, scarcely acute at the apex, sometimes
	very slightly enlarged, very rarely more or less cylindric
2.	Inner corona-lobes glabrous (or virtually so), \pm flat on the truncate apex;
	tube shallow ± half as long as wide, often sparingly asperulate inside;
	corolla-lobes ± deltate; papillae subulate, flattened; stems
	5-angled
	Inner corona-lobes minutely papillose, clavate, ventricose-clavate, inverted
	foot-like, or rarely stoutly obtuse, subcylindric sometimes
_	slightly subclavate
3.	(2) Corolla 30–50 mm diam.; papillae up to 5 mm long; pedicel 20–50 mm
	long: inner corona-lobes usually distinctly foot-like or occa-
	sionally ± hoof-like
	Corolla 20-30 mm diam.; papillae up to 3 mm long; pedicel 12-32 mm
	long; inner corona-lobes truncate, ± hoof-like, usually micro-
	puberulous, often pustulate 1b hystrix var. parvula
4.	(2) Corolla-lobes ± deltate, often wider than long
	Corolla-lobes deltate-acuminate or \pm narrowly triangular, longer
	than wide

5.	Inner corona-lobes at least 2,5 mm long
_	Inner corona-lobes not more than 2 mm long; papillae conical, obtuse, short; stems 4-angled; tube sparingly asperulous inside towards the base; corolla ±
	tubular with sub-erect or sub-erectly spreading lobes
6.	Tube wholly dark purple within, sometimes obscurely somewhat
	palely banded
7.	Corolla tubular or tubular-campanulate; inner corona-lobes sub-
	cylindric, or stoutly obtuse and sometimes slightly subclavate
	conical, up to 2 mm high; inner corona-lobes clavate; stems
8.	4/5-angled
0.	papillae; corolla tubular, scabrous outside, with a raised densely minutely
	papillose annulus inside shortly above the base; stems 4/5-angled
_	Papillae stout, obtuse, without long setae; tube slightly constricted above the
	ampliate base with the throat at least as long as the ampliate portion; corolla-lobes widely spreading, often slightly acuminate;
	stems 5/7-angled
9.	(6) Tube shallow, ± half as long as wide; papillae subulate, flattened; inner corona-lobes clavate, ventricose-clavate, occasionally ± cylindric obtuse,
	rarely inverted foot-like, minutely papillose; stems 5-angled
_	Tube at least as long as wide; papillae elongated conical; inner corona-lobes clavate or sometimes ± cylindric obtuse; stems 4/6-angled
10.	Stems erect or shortly decumbent erect, usually prominently toothed and angled
	Stems trailing with somewhat obsolescent tubercles and rounded
11.	angles
11.	lobes clavate, sub-clavate or sometimes ± cylindric obtuse; corolla often
	slightly ampliate at the base; stems 5/6-angled 15b longituba subsp. cashelensis Papillae without setae, inner corona-lobes clavate, corolla not
	ampliate at the base; stems 4/5-angled 15a longituba subsp. longituba
12.	(4) Stems 4/7-angled; corolla-lobes deltate-acuminate, inner corona- lobes ± 3 mm long or more
_	lobes ± 3 mm long or more
13.	corona-lobes \pm 2 mm long, usually rather knob-like at the apex
	as long as wide; inner corona-lobes usually inverted foot-like, rather bristly
	papillose; stems usually 4-angled, very rarely 5-angled 2 stapelioides
_	Tube wholly dark purple within (sometimes obscurely palely banded), at least as long as wide; <i>inner corona-lobes</i> stout, obtuse, rarely slightly sub-
	clavate, never at all foot-like; stems 5/7-angled 12b hislopii subsp. robusta
14.	2) Stems with 14–20 vertical or spiral rows of tubercles, each tipped
_	with a long soft bristle
, -	17b pillansii subsp. echidnopsioides
15.	(1) Inner corona-lobes subulate, rarely slightly enlarged at the minutely obtuse apex or ± cylindric obtuse, minutely papillose or tuberculate-
	scabrous
	corolla smooth outside, minutely spotted within

16.	$Tube \pm uniformly dark purple inside$
	Tube distinctly concentrically lined or clearly dotted in a labyrinthine pattern (red on whitish)
17.	Stems 5-angled, slender, not more than 10 mm thick, usually trailing; corolla bicampanulate with short conical papillae; corona short with subulate inner
	lobes with their base close to (almost touching) the corona-disc11 occulta
_	Stems 5/7-angled, stout, more than 10 mm thick, erect; corolla ± tubular with widely spreading lobes; papillae stout, obtuse; inner corona-lobes
10 (16)	stoutly subulate or subcylindric
18. (16)	Corolla-lobes deltate to deltate-acuminate
	5-angled
19.	$Tube \pm \text{ cylindric, bowl-shaped or slightly urceolate} \dots 20$
-	Tube conspicuously globose-ampliate, distinctly concentrically lined within, constricted at the throat; corolla-lobes deltate-acuminate, widely spreading,
20.	often recurved
	Stems elongated, prostrate, almost cylindric with obsolescent tubercles,
	usually obtusely 4-angled; pedicel 17,5-30 mm long; corolla 30-45 mm
	diam.; papillae very slender, up to 0,2 mm diam., 2,5 mm long, almost hair-like
21.	Papillae with relatively long setae or bristles
_	Papillae without long setae or bristles
22.	Stems 5/6-angled; papillae provided with acute setae
	Stems 8/9-angled; papillae tipped with a long, stout, obtuse, sometimes
_	subclavate bristle
23.	Stems with 4/5, ± prominently dentate angles
_	Stems with $6/10 \pm$ obtuse \pm tessellate angles; inner corona-lobes 2–2,5 mm
	long
24.	Corolla more than 20 mm diam, with widely spreading deltate-acuminate
	lobes
_	Corolla less than 20 mm diam. (usually ± 12 mm), campanulate, with suberect deltate lobes
25.	Sepals \pm 10 mm \times 1–1,5 mm; corolla \pm 30 mm diam., with lobes \pm 9 mm
	× 9 mm; stems greyish green purplish mottled, with relatively long, very acute teeth
_	
	Sepals \pm 6–7 mm \times 1,25–1,75 mm; corolla 20–25 mm diam., with lobes \pm
	7 mm long $\times \pm 6$ mm wide; stems green with relatively short, acute teeth
26 (22)	7 mm long $\times \pm 6$ mm wide; stems green with relatively short, acute teeth
26. (23)	7 mm $\log \times \pm 6$ mm wide; stems green with relatively short, acute teeth
26. (23)	7 mm long $\times \pm 6$ mm wide; <i>stems</i> green with relatively short, acute teeth
26. (23) —	7 mm long × ± 6 mm wide; stems green with relatively short, acute teeth

GROUP I

In addition to the obviously closely related and characteristically papillose *H. hystrix*, *H. stapelioides* and *H. volkartii*, and despite the extent of discontinuity apparent from its morphology, *H. loesenerana* is included in this group as it appears to be more closely related here than elsewhere, and is sometimes only



somewhat doubtfully distinguished from the contiguously distributed H. stape-lioides.

It seems probable that the extremely variable *H. hystrix* may be ancestral to this group and that differentiation has occurred more or less on the periphery of its distribution, with somewhat similar combinations of characters emerging at different points. For example: plants of var. *parvula* from the Port Shepstone area, and others from the northern Transkei appear to exhibit a rather closer affinity with *H. stapelioides* and *H. volkartii* than do most more typical specimens of *H. hystrix*.

The species of this group, although very variable in some of their characters, are sufficiently constant in others to be readily identifiable and are, in addition,

separated to a very large extent both ecologically and altitudinally, and in the tetraploid *H. volkartii* by its disjunct distribution also.

 $H.\ hystrix$ occupies low altitude areas, generally below 750 m, while $H.\ stapelioides$ occurs at middle altitudes up to \pm 1 500 m and $H.\ loesenerana$ at about 1 250 m and above. There is some merging, in the Transvaal, of the distributions of $H.\ hystrix$ and $H.\ stapelioides$ at their respective upper and lower altitudinal levels, and it seems possible that the occasionally spiny and very rarely 5-angled stems of some specimens of $H.\ stapelioides$ may be due to hybridisation, although there seems little or no evidence of this in floral characters. The distribution of $H.\ volkartii$ is entirely tropical, with records mainly from Rhodesia and Angola.

1. Huernia hystrix (Hook.f.) N.E.Br. in Gard. Chron. 5: 795 (1876).—K. Schum., Asclepiadaceae in Engler & Prantl, Pflanzenfam. 4 (2): 280 (1895), "Heurnia".—Schlechter in J. Bot. 36: 485 (1898).—N.E.Br., Asclepiadaceae in Thistleton-Dyer, Fl. Cap. 4 (1): 911 (1909).—Berger, Stap. u. Klein.: 172 (1910), "Heurnia".—J. M. Wood, Natal Plants 6 (3): t. 556 (1912).—Gomes e Sousa in Moçambique 4: 45, 47 (1935) et 49: 61 (1947). "histryx".—White & Sloane, Stapelieae, ed. 2, 3: 892 (1937).—Phillips in Flower Pl. S. Afr. 19: 757 (1939).—O. West, Veg. Weenen County, Natal: 145 (1948).—Luckhoff, Stap. S. Afr.: 208 (1952).—Jacobsen, Handb. Succ. Pl. 2: 622 (1960) et Lexicon Succ. Pl.: 274 (1974).—Compton, Checklist Flora Swazil.: 64 (1966).—D. Edwards, Pl. Ecology Survey Tugela R. Basin: (1967).—Plowes in Excelsa 1: 16, 30 (1971).—Ross, Flora Natal: 292 (1972).

Type: Natal, M'Ken s.n.; Icon.: W. Fitch in Bot. Mag.: t. 5751 (1869).

Stapelia hystrix Hook.f. in Bot. Mag.: t. 5751 (1869).

Type: as above.

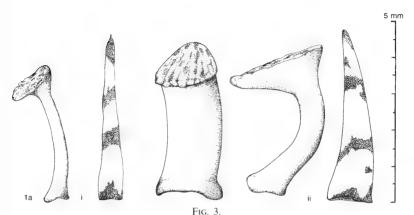
Huernia appendiculata Berger, Stap. u. Klein.: 174 (1910), "Heurnia".

Type: "S. Africa ?". Locality unknown.

Huernia hystrix var. appendiculata (Berger) White & Sloane, Stapelieae, ed. 2, 3: 898 (1937).—Jacobsen, Handb. Succ. Pl. 2: 622 (1960), et Lexicon Succ. Pl.: 274 (1974).

Type: as above.

Var. appendiculata is here considered to be synonymous with the typical variety as from Berger's figure it appears to be based on a more or less normal flower with its corona in the early stages of collapse. The terminal appendages of the inner lobes of the corona depicted are perhaps longer than most, but as the size and shape of these appears to be almost infinitely variable this is not considered to be of any significance. It should perhaps here be explained that in the early stages of the collapse of huernia flowers the inner corona-lobes appear to be affected first, in most species becoming more divergent and recurved, sometimes rather sharply so towards the apex (e.g. see Schlechter's sketch of *H. stapelioides*, White



 H. hystrix var. hystrix. (i) Fawnleas, Natal, Bayer s.n. (ii) Nelspruit, Transvaal, Leach 14133 (exceptionally large corona-lobe and papilla).

& Sloane *l.c.*). This effect is accentuated in var. *hystrix* by the normally horizontally positioned "foot-like" terminal appendage then becoming vertically arranged with the "heel" erect.

Despite the variability of some of its characters *H. hystrix* is almost always easily distinguished from its immediate relatives by its sprawling rather than tufted habit, its relatively long pedicel (in var. *hystrix* normally at least twice as long as those of *H. stapelioides* and *H. volkartii*), and humifuse flowers.

Two varieties are recognized, of which the typical is by far the more widely distributed, while var. *parvula* appears to be restricted to a relatively small area of south-eastern Natal where var. *hystrix* is not known to occur. The new variety could perhaps, on this account, be considered to qualify for subspecific rank, but in view of the existence of intermediates such as *Codd 5941* from Tugela Ferry, and others, mainly from the northern Transkei, it is considered that varietal status is more appropriate.

It was at first thought that the rather small flowers of Fitch's drawing (Bot. Mag. *l.c.*) might represent this new variety; however, the description and other details of the figure leave no doubt that the generally larger flowered typical variety is depicted. Unfortunately none of the original material has been traced.

a. var. hystrix

Chromosome number: 2n = 22, Reese u. Kressel (1967) and Focke Albers (1975).

RHODESIA—S: Sabi/Lundi Junction, Chitsa's Kraal, H. Wild 3504 (SRGH); Gona re Zhou Nat. Park, fl. Feb. 1969 (SRGH), ibid. cult. Umtali sub Plowes

- 3011, Broadley s.n. (PRE), ibid. cult. Greendale, sub Leach 14233, Blake 119 (SRGH).
- MOÇAMBIQUE—SS: Caniçado, cult. Nelspruit, sub *Leach 12293*, fl. i.1965, *Mockford s.n.* (SRGH).
- —LM: Catembe, cult. C.I.C.A., Lourenço Marques, fl. 27.i.1955, Lemos 65 (LMA); Polana, fl. 21.x.1963, Balsinhas 622 (LMA), ibid, fl. 15.i.1946, A. de Sousa 236 (PRE); Lourenço Marques, cult. PRE, fl. iv.1937, F. v.d. Merwe 405 (PRE); = 16 km N of Moamba, Leach & Bayliss 12256 (SRGH), ibid. cult. Nelspruit, fl. i.1965, Leach & Bayliss 12254 (BOL, K, LISC, MO, NBG, PRE, SRGH).
- SWAZILAND—2531 (Komatipoort): ± 15 km N of Bordergate (-DD), fl. 23.xii.1960, Leach & Bayliss 10604 (PRE, SRGH).
- —2631 (Mbabane): ± 24 km SE of Manzini (Bremersdorp) (-DA), fl. 25.xii.1960, Leach & Bayliss 10615 (PRE); Mhlatuze Riv. (-DC), Leach & Bayliss 10630 (SRGH); "bushveld near Stegi, 1000" ", cult. Mbabane, fl. xii.1960, M. Karsten s.n. (NBG).
- —2731 (Louwsberg): Maloma (-BA), cult. Nelspruit sub *Leach 12241, G. W. Reynolds s.n.* (BOL, PRE); Ingwavuma Poort (-BB), cult. NBG, fl. 23.i.1963, *H. Hall 2339* (NBG).
- S. AFRICA. TRANSVAAL—2229 (Waterpoort): Wyllie's Poort (-DD), cult. PRE, fl. 4.xii.1954, *Codd 8353* (PRE); north side of Zoutpansberg (-DD), cult. Umtali, various dates, *Plowes 2607* (K, NBG, SRGH).
- —2329 (Pietersburg): Bandolier Kop (-BD), cult. & fl. Umtali, 3.ii.1967, *Plowes 2473* (PRE); Kalk Bank (-CB), fl. v.1926, *Farquhar s.n.* (GRA); Pietersburg (-CD), cult. NBG 1520/48, fl. 30.iii.1949, *Kransdorff s.n.* (NBG); Louis Trichardt, cult. PRE, fl. iii.1912, *Gettliffe* (GRA).
- —2330 (Tzaneen): Mokeetsi (-CA), cult. Nelspruit, various dates, *Leach 12019* (BOL, BR, MO, LISC, SRGH, ZSS); ibid. fl. 21.xii.1932, *Schweickerdt 1051* (PRE), idem cult. PRE, fl. xii.1933, *Schweickerdt s.n.* (PRE); between Soekmekaar & Munnik, *Leach 9836* (SRGH); "Woodbush" (-CC), fl. xii.1907, *Gough 3884* (PRE).
- —2430 (Pilgrim's Rest): Shilovane (-AB), *Junod 4140* (PRE); Burgersfort (-CD), cult. Nelspruit Bot. Gard., fl. 15.iv.1973, *Buitendag 1007* (NBG, PRE).
- —2529 (Witbank): Klipspruit/Olifants Riv. Junction (-CA), fl. iii.1947, *Thomalla* in PRE 43946 (PRE).
- —2530 (Lydenburg): ± 8 km S of Nelspruit (-DB), cult. & fl. Greendale, xii.1975, *Leach 14133* (BOL, K, MO, PRE, SRGH); Nelspruit (-DB), *Rogers 24491* (GRA).
- —2531 (Komatipoort): 7 mls S of Pretorius Kop (-AA), cult. PRE, fl. 30.iii.1953, Codd 6501 (PRE), & fl. ii.1954, Codd 5923 (PRE); Plaston (-AC), fl. iii.1932, Holt 218 (PRE); Malelane (-AC), fl. 6.iii.1965, Leach & Bayliss 12731, fl. v.1965, Leach & Jones 12852 (SRGH); Louws Creek (-CB), fl. 3.vii.1914,

- Edwards s.n. (PRE); Kaapmuiden (-CB), cult. Greendale, Leach 9814 (SRGH); Barberton (-CC), fl. i.1912, Thorncroft 11122 (PRE), idem 4253 (SAM).
- NATAL—2632 (Bela Vista): 5 mls NE of Makane's Drift (-CD), fl. 6.iii.1970, Ross 2363 (ND, PRE, SRGH).
- —2731 (Louwsburg): Pongola Poort, cult. Nelspruit, fl. i.1965, *Ward* sub *Leach* 12197 (PRE).
- —2732 (Ubombo): Ingwavuma (-AA), cult. Umtali, fl. 22.xi.1971, *Strey* sub *Plowes 3012* (ND); Makatini Flats, Pongola (-CA), *Strey s.n.*, cult. Umtali sub *Plowes 3013* (SRGH); Makatini Flats, below Ubombo (-CA), cult. NBG, fl. 12.xi.1971, *Wisura 1191* (NBG).
- —2829 (Harrismith): Mielietuin Siding (-DD), fl. 19.iii.1970, Strey 9750 (ND).
- —2830 (Dundee): Blaauwkrantz Riv. Valley (-CC), fl. 19.xi.1943, Acocks 9912 (ND); "Onverwacht", fl. 11.ii.1945, Acocks 11226 (PRE); Muden Valley, cult. Johannesburg, Reynolds 354 (PRE); Weenen, fl. i.1941, Schelpe in ND 3322 (ND), fl. 15.iii.1933, Symons in Transv. Mus. 31812 (PRE); Muden (-CD), Bulawayo Mus. 37 (SRGH); Tugela Ferry, Bulawayo Mus. 13 (SRGH); 2 mls S of Tugela Ferry, fl. 9.iv.1950, Codd 5941 (PRE).
- —2831 (Nkandla): Ntambana Valley, 20 mls W of Empageni (-DC), cult. NBG 42/44, fl. 3.iii.1944, *Houting s.n.* (NBG); Umhlatuzi Valley, Melmoth Road, 23.vii.1949, *Lawn 884* (ND).
- —2832 (Mtubatuba): near Mtubatuba (-AC), fl. 1.iv.1948, Rodin 4222 (PRE).
- —2930 (Pietermaritzburg): Nottingham (-AC), fl. 15.vii.1940, *Mercer s.n.* (PRE); Wartburg (-BC), fl. 14.viii.1966, *Plowes 2596* (ND), idem cult. Umtali (PRE, SRGH); Inchanga (-DA), *Leach 5406* (SRGH); Umgeni Riv. (-DB), fl. 10.viii.1969, *Strey 8837* (ND); Umlaas Riv., Camperdown (-DC), fl. & fr. 21.x.1910, *Franks* sub *Medley-Wood 11717* (Natal Pl. 6: t. 556) (ND), ibid. fl. 1934, *Reynolds 354A* (PRE).
- —"Natal": Medley-Wood 4970, cult. ND, fl. 4.iii.1891 (ND); Pillans 25 (GRA).
- —2931 (Stanger): Kranskop (-AA), cult. Umtali, fl. 26.iv.1975, *Bayer* sub *Plowes* 4200 (NBG); Mpisi Riv., Tugela Valley, fl. 3.iii.1962, *Edwards* 2732 (PRE).
- CAPE—3029 (Kokstad): Kokstad (-CB), *Bulawayo Mus. 53* (SRGH); Umzimvubu Riv., E of Mt. Frere (-CC), *Plowes 3271* (SRGH).
- —3128 (Umtata): Tsitsa Falls (-BD), cult. PRE 4769/5/39, McLoughlin s.n. (PRE); Umtata (-DB), cult. PRE 43948, McLoughlin s.n. (PRE).
- "Transkei" cult. NBG 26/67, 3.iii.1971, M. Holmes s.n. (NBG).

Plant: usually rather sprawling with loosely linked stems, sometimes forming quite large patches.

Stems: decumbent-erect, usually \pm 60–70 mm long, 5-angled, sharply sulcate, with the angles strongly tuberculate-dentate, often spiny from the hardened, acute tips of the teeth.

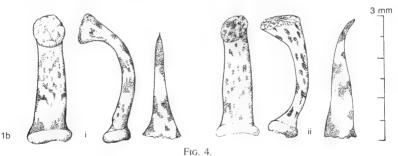
Pedicel: terete, tapering slightly towards the apex, (20) 30–50 (60) mm long, usually extended clear of the stems with the flower lying flat on the soil.

Sepals: ovate-acuminate, obtusely keeled, 7-10 mm long, 1,5-2,5 mm wide.

Corolla: subrotate with the limb and lobes abruptly, widely spreading, (30) 35–50 mm diam., buff-coloured to yellowish, scabridulous outside; inside marked with brown-red spots and lines; papillae fleshy, subulate, flattened, with or without a minute mucro, up to 3,5–5 (5,5) mm high, usually \pm 1 mm broad at the base; tube shallowly pan-shaped, usually less than half as deep as broad, often sparingly asperulous inside towards the base; lobes more or less deltate, sometimes wider than long, occasionally shortly attenuate, often recurved (I have not seen any which could be described as long and narrow and suspect that the note by White & Sloane (l.c.) may refer to misidentified specimens of H. stapelioides).

Corona: outer lobes extremely variable in shape and colour, sometimes absent; inner lobes erect, dorsiventrally much compressed, strap-like and almost parallel-sided, abruptly horizontally expanded at the apex into a generally more or less inverted foot-shaped appendage, which is glabrous or rarely micro-puberulous; the shape and size of this appendage is almost infinitely variable, although conforming always, albeit sometimes somewhat vaguely, to an inverted foot pattern which may be ovate or obovate, "pointed" or "square-toed", with the "heel" longer than the "toe" or almost entirely lacking, while the upper surface may be flat, pustulate-rugulose or sulcate or sometimes a combination of these; nectarial orifice partially concealed by a rather broad but not very prominent tubercle.

Pollinia: elliptic-oblong, 0,35–0,52 (0,56) × 0,23–0,32 mm.



1b. H. hystrix var. parvula. (i) Izingolweni, Natal, Strey 6139. (ii) Oribi Flats, Natal, Strey 9730.

b. var. **parvula** Leach, var. nov. ab varietate typica differt planta omni minore, caulibus brevissimis; inflorescentia prope basin vel secus caules interdum etiam prope apicem temere exorienti; floribus minoribus, corollae papillis brevioribus et coronae lobis interioribus truncato-clavatis (non valde abrupte plano-ampliatis).

Typus: S. Africa, Natal, Oribi Flats, R. G. Strey 9730 (K, MO, PRE, holo., SRGH).

Chromosome number: 2n = 22, Lavranos 7667 (KIEL), Focke Albers (1975).

S. AFRICA. NATAL—3030 (Port Shepstone): Oribi Flats, overlooking Umzilkulwana Valley (-CA), 29.vii.1953, *Dyer 5415* (PRE); Oribi Gorge (-CB), cult. Umtali, fl. i.1974, *Plowes 2648* (LISC, PRE); 8 km NW of Umtentweni, cult. Umtali, fl. xi.1968, *Plowes 2645* (BOL; SRGH); Oribi Flats, "Gibraltar" (-CB), *R. G. Strey 9730*, cult. Greendale, sub *Leach 14464* (K, MO, PRE, SRGH), cult. Umtali, sub *Plowes 4255* (ND); Izingolweni (-CC), cult. Umtali sub *Plowes 3136*, fl. 10.v.1969, *Strey 6139* (SRGH).

Stems: 5-angled, seldom more than 30 mm high.

Pedicel: 14-32 mm long, averaging 17,5 mm.

Sepals: $5-8 \text{ mm} \times 1,25-1,75 \text{ mm}$.

Corolla: closely similar to that of the typical variety but smaller in all its parts, 30–35 mm diam., with papillae usually \pm 2,5 mm high (rarely up to 3 mm); buds more conical than in var. hystrix.

Corona: inner lobes rather less strap-like and less abruptly expanded at the truncate-clavate (often obliquely so) apex with a greater tendency to be puberulous and pustulate-rugulose on the upper surface.

Var. parvula is quite well distinguished by its smaller stature with very much shorter stems; its variably positioned inflorescence (sometimes near the apex of the stems); its smaller flowers with shorter papillae and rather different inner coronalobes which are less abruptly expanded at their truncate-clavate apex. It has sometimes been suggested that it should be recognized as specifically distinct from H. hystrix; however, in 5-angled stems; relatively long pedicels; "shaggy" flowers with a shallow tube which is sometimes sparingly asperulate inside; relatively long, subulate papillae and glabrous or puberulous, not at all papillose, inner corona-lobes, its overall similarity to H. hystrix is such that it can scarcely be considered other than of infraspecific standing and in view of the circumstances previously outlined it is considered that varietal status best reflects the situation.



Fig. 5.
2. H. stapelioides. (i) Groblersdal, Transvaal, Plowes 4204. (ii) Buffelsvlei, Transvaal, Leach 12084. (iii) Hammanskraal, Transvaal, Plowes 2609.

2. Huernia stapelioides Schlechter in Bot. Jahrb. 20 (Beibl. 51): 55 (1895) et Journ. Bot. 36: 485 (1898).—N.E.Br., Fl. Cap. 4 (1): 922 (1909).—Berger, Stap. u. Klein.: 167 (1910).—White & Sloane, Stap. ed. 2, 3: 899 (1937).—Jacobsen, Handb. Succ. Pl. 2: 629 (1960) et Lexicon Succ. Pl.: 277 (1974).—Compton, Checklist Flora Swazil.: 64 (1966).

Type: Nazareth, between Houtboschberg & Klippdam, Schlechter 4487 (B†).

Huernia vogtsii Phillips in Flower. Pl. S. Afr. 12: t.452 (1932).—White & Sloane, Stap. ed. 2, 3: 901 (1937).—Luckhoff, Stap. S. Afr.: 209 (1952).—Jacobsen, Handb. Succ. Pl. 2: 631 (1960) et Lexikon Succ. Pl.: 277 (1974).

Type: Crocodile Poort, Magaliesberg, L. R. Vogts No. 10144 in Nat. Herb. (PRE!), (single flower only).

Chromosome number: 2n = 22 - Focke Albers (1975).

Although no specimen seen by Schlechter has been traced, it is, in view of the scantiness of material from the area of the type locality, deemed to be advisable to leave the selection of a neotype in abeyance in the hope that more adequately representative material may be obtained from this area.

- S. AFRICA. TRANSVAAL—2229 (Waterpoort): Alldays (-CA), cult. Nelspruit sub *Leach 12218, Schlieben 9213* (PRE).
- —2327 (Ellisras): Ellisras (-DA), cult. Umtali sub *Plowes 3131, Haagner s.n.* (PRE).
- —2329 (Pietersburg): "Louis Trichardt" (-BB), fl. iv.1911, Gettliffe 9780 (PRE); 32 km N of Pietersburg (-CB), cult. NBG 1573/48, fl. 14.ii.1949, Kransdorff s.n. (NBG); Kalkbank (-CB), Obermeyer et al. in Herb. Transv. Mus. 31801 (PRE); Pietersburg (-CD), cult. Nelspruit sub Leach 12818, Strauss s.n. (SRGH), ibid. Plowes 1911 (SRGH); Boyne (-DD), cult. Umtali, fl. 29.i.1967, Plowes 2610 (BOL); 32 km E of Pietersburg (-DD), cult, NBG 510/1954, fl. 29.iii.1956, H. Hall s.n. (NBG).
- —2428 (Nylstroom): Naboomspruit (-DA), cult. Pretoria, fl. iv.1932, *Schweickerdt* in Herb. Transv. Mus. *30643* (PRE).
- —2429 (Zebediela): 9 km S of Pietersburg (-AB), cult. Johannesburg, fl. 12.ii.1936, *Reynolds 1523* (PRE); Naauwpoort (-BC), *Obermeyer et al.* in Herb. Natal *27631* (ND); 5 km E of Chunies Poort (-BC), cult. Johannesburg, fl. 12.ii.1935, *Reynolds 1350* (PRE).
- —2430 (Pilgrim's Rest): Brandraai (-BA), cult. Nelspruit, Leach 12837 (BOL, K, SRGH); Burgersfort (-CB), cult. Umtali sub Plowes 3592, fl. ii.1973, Hardy s.n. (K, PRE); 24 km W of Steelpoort (-CC), cult. Nelspruit, fl. iii.1964, Leach &

Bayliss 12084 (B, BOL, BR, K, PRE), ibid. cult. NBG, fl. 16.i.1964, Bayliss & Leach 1469 (NBG), ibid. cult. Nelspruit, fl. 14.ii.1964, Leach & Bayliss 12086 (SRGH), "Sekukuniland", cult. NBG 529/56, fl. 7.ii.1957, H. Hall s.n. (NBG). —2527 (Rustenburg): Crocodile Poort (-DD), cult. PRE, fl. i.1932, Vogts in PRE 10144 (PRE).

—2528 (Pretoria): 10 km W of Hammanskraal, cult. Greendale, fl. 6.iii.1960, Leach 9813 (PRE, SRGH), ibid., fl. xi.1934, Retief s.n. (BOL); 6 km W of Hammanskraal, cult. Umtali, Plowes 2609 (K); 3 km N of Pyramids Stn. (-CA), cult. PRE, fl. ii.1937, Mogg s.n. (PRE).

—2529 (Witbank): Groblersdal (-AB), cult. Umtali, fl. 13.ii.1973, *Plowes 4204* (SRGH), ibid., fl. 18.xii.1968, *Plowes 3277* (PRE).

SWAZILAND—2632 (Bela Vista): Ubombo Hills, 16 km from Stegi (-AA), fl. 28.iii.1935, *Keith s.n.* (PRE); ± 24 km S of Stegi, fl 28.xii.1960, *Leach & Bayliss 10646* (SRGH); ± 25 km S of Stegi, cult. NBG, fl. 5.ii.1962, *Compton 28044* (NBG).

Plants forming rather squat compact clumps; *stems* 4/5-angled, stout, usually turgid and almost square (5-angled apparently very rare), with the angles tuberculate dentate, rarely with the tips of the teeth hardened and spine-like.

Pedicel: 7–18, usually \pm 10 mm long.

Sepals: attenuate, obtusely keeled, $8-10 \text{ mm} \times 1-1,5 \text{ mm}$.

Corolla: buff to yellowish, 30–42 mm across the tips of the widely spreading lobes, somewhat scabridulous outside, inside marked with maroon spots and lines; papillae subulate, flattened, up to 2,5 mm long; tube smooth inside, bowl or cup-shaped, $\pm 1\frac{1}{2}$ times as wide as long; lobes deltate-acuminate (sometimes almost deltate-caudate), usually $\pm 1\frac{1}{2}$ times as long as broad.

Corona: inner lobes erect, 2,5–3,0 mm long, dorsiventrally compressed, very variably enlarged at the convex, conspicuously "bristly" papillose apex, clavate, ventricose-clavate or, most commonly, shaped somewhat like an inverted foot; nectarial orifice almost concealed by a broad obtuse tubercle.

Pollinia: oblong-elliptic, 0,35–0,5 mm × 0,25–0,35 mm.

H. stapelioides is occasionally, but somewhat unaccountably confused with H. hystrix, from which it is immediately distinguishable by its more compact habit with stout, 4-angled stems (5-angled stems appear to be very rare, I have seen only one such specimen, Leach 12837 from Brandraai), its very much shorter pedicels, differently proportioned corolla (most evident in bud), with a proportionally longer tube and more acuminate proportionally longer lobes which are covered with shorter, although otherwise similar papillae, and finally and most conclusively by its very different "bristly" papillose inner corona-lobes.

An excellent account of this species by J. F. Kirsten is to be found under *H. vogtsii* in White & Sloane (1937).

3. Huernia loesenerana Schlechter in Bot. Jahrb. **20** (Beibl. 51): 55 (1895), et in Journ. Bot. **36:** 485 (1898).—N.E.Br., Fl. Cap. **4** (1): 911 (1909).—Berger, Stap. u. Klein.: 171 (1910).—Phillips in Flower. Pl. S. Afr. **6:** t.216 (1926).—White & Sloane, Stap. ed. 2, **3:** 905 (1937).—Jacobsen, Handb. Succ. Pl. **2:** 624 (1960), et Lexicon Succ. Pl.: 275 (1974), "loeseneriana".

Type: S. Africa, Transvaal, near Olifants Riv., \pm 5 000 ft. alt., 20.xi.1893, Schlechter 3774 (B \dagger).

Chromosome number 2n = 22 - G. Reese (1971) & Focke Albers (1974).

Schlechter's type specimen was destroyed in Berlin and neither isotype material nor any other specimen seen by Schlechter is known to exist. However, as with *H. stapelioides*, the selection of a neotype is left in abeyance, as none of the scanty available specimens is considered to be really adequate for this purpose. The holotype from 'near Olifant's River' appears to have been collected in the vicinity of Middelburg and the only specimen seen from this locality (*Buys* sub *Plowes 3283*) is an aberrant plant with albino flowers which is consequently considered to be unsuitable for typification purposes.

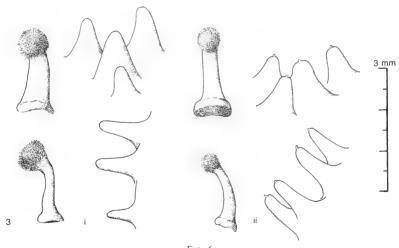


FIG. 6.
3. H. loesenerana. (i) Middelburg, Transvaal, Buys sub Plowes 3283. (ii) Witbank, Transvaal, Plowes 2629.

S. AFRICA. TRANSVAAL—2428 (Nylstroom): Warmbaths (-CD), cult. Pretoria, fl. iv. 1912, *Leendertz 11462* (PRE).
—2527 (Rustenburg): Rustenburg Distr., cult. NBG 492/56, fl. 26.xi.1956, *H*.

Hall s.n. (NBG).

—2528 (Pretoria): Aapies Riv. (-CA), fl. ii.1904, Bolus 11119 (BOL), ibid. fl. 30.ix.1909, Leendertz 2101 (GRA) et 7210 (PRE); between Riviera & Gezina (-CA), fl. iii.1930, Nouhuys sub PRE 8458 (PRE); hilltop, Riviera (-CA), fl. 18.xii.1925, Smith 1825 (PRE); Sunnyside, Pretoria, fl. x.1913, Stent sub PRE 43945 (PRE); Brooklyn, Pretoria, fl. v.1935, Verdoorn s.n. (PRE); Brummeria (-CB), Prins s.n. (PRE); Irene, kopje E of rly. (-CC), Obermeyer 442 (PRE).

—2529 (Witbank): 5 km N of Witbank (-CC), cult. Umtali, fl. vi.x.1968, *Plowes 2629* (K, PRE); near Middelburg (-CD), cult. Umtali, fl. i.1972, "albino", *Buys sub Plowes 3283* (SRGH).

—2530 (Lydenburg): 8 km SE of Waterval Boven (-CB), cult. PRE, fl. 1937, Reynolds 2155 (PRE); Waterval Boven, cult. GRA, Britten 4813 (GRA); Waterval Boven Tunnel, fl. 1.iii.1937, F. v. d. Merwe 1248 (PRE).

—2627 (Potchefstroom): Sterkfontein Caves (-BA), fl. 25.xii.1969, *Mogg 34666* (J); Magaliesburg (-AB), cult. PRE, fl. 12.iv.1964, sub *Leach 12161* (SRGH).

—2628 (Johannesburg): Rivonia (-AA), fl. 24.iii.1958, *Lavranos s.n.* (PRE); Kloof, Heidelburg (-AD), cult. Umtali, fl. i.1972, *Plowes* 2909 (NBG, PRE).

ORANGE FREE STATE—2627 (Potchefstroom): Witkop near Parys (-DC), cult. Umtali sub *Plowes 3593*, fl. Jan. 1972, *W. J. Louw s.n.* (SRGH).

Plant tufted; *stems* short (usually less than 6 cm long), stout relative to their length, with 4 acute, dentate angles.

Pedicel: 2–10 mm (usually \pm 7 mm) long.

Sepals: narrowly ovate-attenuate, 4–7,5 mm \times \pm 2 mm.

Corolla: campanulate, 18–26, usually \pm 20 mm diam., buff to brownish coloured, scabridulous outside, inside densely marked with brown to dark crimson, broken transverse lines and spots, papillae short, stout, obtusely conical, somewhat widened at the base, up to \pm 1 mm long, rarely shortly apiculate; *tube* more or less cup-shaped, widening slightly towards the throat but not at all urceolate, \pm 10 mm diam., 7–9 mm long, sparingly asperulous towards the base inside; *lobes* broadly deltate, 5–6,5 mm long, 6,5–9 mm wide at the base, suberectly or sometimes widely spreading, but not abruptly so, intermediate lobes small, \pm 1,5 mm long.

Corona: outer lobes somewhat variable, mostly more or less subquadrate, obtuse or subtruncate; inner lobes erect or sometimes connivent-erect, short, usually \pm 1,75 mm long, transversely ridged at the base, clavate, minutely papillose at the knob-like apex; nectarial orifice concealed by a prominent tubercle.

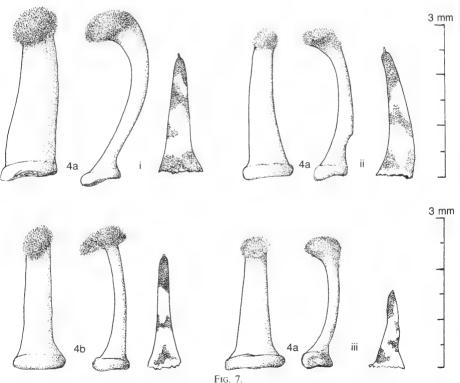
Pollinia: oblong-elliptic, 0,4–0,5 mm \times 0,25–0,3 mm.

Schlechter's note regarding the exceptional length of the corolla-tube and its comparison with that of *Tavaresia* is rather mystifying as this is not supported by the available material nor by Schlechter's description in which the length of the whole corolla is given as 1,5 cm.

Although superficially resembling *H. stapelioides* and having a contiguous distribution, this species is easily distinguished therefrom by its proportionally longer more open tube which is asperulous inside towards the base; its proportionally shorter and wider, more or less triangular corolla-lobes which are usually wider than long, and especially by its much shorter obtusely conical papillae and short clavate inner corona-lobes which are usually very knob-like at the apex.

4. Huernia volkartii Peitsch. ex Werderm. & Peitsch. in Gartenflora **85:** 78 (1936), "Heurnia".—R. A. Dyer in Flower. Pl. Afr. **38:** t.1519B (1967), p.p. excl. var. *nigeriana*.—Jacobsen, Lexicon Succ. Pl.: 277 (1974), p.p. excl. var. *nigeriana*.

Huernia volkartii Peitsch. in Gartenflora 85: 9, 10 (1936) nom. nud.



4a. H. volkartii var. volkartii. (i) Mt. Emberengwa, Belingwe, Rhodesia, Leach 14879. (ii) Chimanimani Mtns., Rhodesia, Plowes 2598. (iii) Gabela, Angola, Leach & Cannell 13951. 4b. H. volkartii var. repens. Espungabera, Moçambique, Percy-Lancaster 74.

Type: Angola, without precise locality, cult. Jena Botanic Gardens.

It appears that no material has survived and the small photograph published by Peitscher is considered to be inadequate for lectotypification purposes.

Huernia volkartii Gossweiler ex White & Sloane, Stap. ed. 2, 3: 907 (1937.— Jacobsen, Handb. Succ. Pl. 2: 631 (1960) et Sukk. Lexikon: 245 (1970), p.p. excl. var. nigeriana.—Huber, Asclepiadaceae in Merxmüller, Prodr. Flora Südwestafrika 114: 40 (1967).—Plowes in Excelsa 1: 16 (1971), p.p. maj.

Type: Angola, Cuanza Sul Distr., Gossweiler s.n. cult. Pasadena. No specimen preserved.

Huernia montana Kers in Bot. Notis. 122: 179 (1969).—Jacobsen, Lexicon Succ. Pl.: 275 (1974).

Type: Angola, Serra da Chela, Kers 3460 (S!).

As all the available Angolan material differs from the original description, particularly in respect of stem characters, it is considered that selection of a neotype should await the availability of material from the area of Vila Nova de Seles, which appears very probably to be the type locality.

The epithet "volkartii" was first used by Peitscher in his article "Sukkulente Kleinodien" in Gartenflora 85, in the caption below the photograph of a plant flowering in Jena Botanic Gardens. This plant was brought from Angola by an unnamed German traveller, and it seems that Werdermann's supposition (Nachtrag zu "Sukkulente Kleinodien" in Gartenflora 85) that the plant was discovered by Gossweiler and that it was provisionally named by him is almost certainly correct. It is quite evident that neither Werdermann nor Peitscher had any knowledge of the origin of the epithet since "the literature was searched and enquiries made". It also seems noteworthy that although 4-angled stems appear to be rare and possibly restricted to Angola, both the original plants had a proportion of such stems, which seems to suggest the possibility that the two plants were actually of clonal origin from Gossweiler's original gathering.

Would it be stretching the long arm of coincidence too far to suggest that the doubtful record of this species from Ovamboland (which is suspected possibly of being subject to horticultural recording errors) which came to Pretoria indirectly through the agency of a Mr. Triebner of Windhoek, might also be from the same stock? These specimens also displayed some 4-angled stems, and there is a long history of fanciers and nurserymen in Windhoek, most of whom came originally from Germany and who almost certainly had contacts with similarly interested persons in that country. Similar "tangles" due to cultivated plants are not uncommon in relation to succulent plants and *H. volkartii* is known to have been quite widely distributed among growers in southern Africa.

H. volkartii appears to be most closely related to H. stapelioides but differs in its more slender 5-angled stems (4/5-angled in the original description, but

4-angled appear to be very rare) as opposed to the almost universally 4-angled, relatively stout stems of *H. stapelioides*, and in its smaller, more open flowers, with a proportionally wider tube (in this approaching *H. hystrix*) and proportionally shorter, less acuminate corolla-lobes (most evident in bud), while the more obtuse, minutely papillose (less ''bristly'') inner corona-lobes are generally diagnostically conclusive, especially in dried material.

The two species are ecologically as well as spatially separated, with *H. stapelioides* occupying rather drier habitats, often in shade of thorn scrub and usually at lower altitudes, while *H. volkartii* is usually found on granite or quartzite, often closely associated with *Selaginella*, in areas of relatively high rainfall, and mostly within the mist belt on mountains and escarpments. Their recognition as distinct at specific level is further supported by the available cytological evidence, on which *H. stapelioides* is shown to be diploid while both varieties of *H. volkartii* are tetraploid.

There is considerable variation in the shape and size of the papillae of *H. volkartii*, with a tendency for these to be more conical, or, more rarely, more nearly terete (i.e. less flattened) than in either *H. hystrix* or *H. stapelioides*. While this tendency appears to be rather more prevalent in material from Angola it is by no means restricted to specimens from that country. The flowers of Angolan plants are also generally rather smaller than of those from Rhodesia and Moçambique, but variation in this respect, even in single gatherings, is such that it is probably not of taxonomic significance.

It has been suggested (Plowes, 1971) that plants from the Natal south coast probably belong here, but these are immediately to be distinguished by their much longer pedicels; quite different, not papillose, truncate inner corona-lobes, and a tube which is often asperulate towards the base inside, while although not so clearly diagnostic, there is a tendency for the papillae of the Natal plants to be longer (particularly those towards the margins and apex of the corolla-lobes) than those of *H. volkartii*. All these distinguishing features are characteristic of the extremely variable *H. hystrix* in which the southern Natal plants are considered to belong.

H. nigeriana Lavranos, which was subsequently considered by its author to be of varietal rank in H. volkartii, is herein reinstated at specific level and is discussed thereunder.

a. var. volkartii

The typical variety is distinguished by its relatively short, erect or shortly decumbent-erect stems with tuberculate-dentate angles.

Chromosome number: 2n = 44, Reese (1971).

ANGOLA. CUANZA SUL DISTR.: "Whaleback" ± 11 km E of Gabela, cult. Nelspruit, fl. 24.ii.1968, *Leach & Cannell 13951* (SRGH); granite outcrop ± 15

km W of Quibala, cult. Nelspruit, fl. 24.ii.1968, Leach & Cannell 13955 (SRGH); "whaleback" ± 20 km W of Quibala, cult. Johannesburg & Pretoria, fl. 1959–60, Reynolds 9372 (PRE); the specimen, N. R. Smuts 1542, cult. PRE, fl. vii.1959 (PRE), and cult. Nelspruit sub Leach 12206 (SRGH), is also considered probably to belong here although reputed to be from Pungo Andongo in Malanje Distr. According to a note by Reynolds, some material of the Quibala gathering was given to PRE by Dr. Smuts, for cultivation there and it is suspected that this was erroneously recorded as from Pungo Andongo, which is the type locality for H. similis and from where there is no record of H. volkartii.

HUILA DISTR.: Humpata, Lubango, Buraco do Bimbe, fl. 22.iv.1960, *Mendes 3770* (LISC); ibid., fl. 22.iv.1960, *Mendes 1487* (LISC); 'road to Tundevala, ± 24 km NW of Sá da Bandeira, fl. 30.iv.1968, *Kers 3460* (S).

SOUTH WEST AFRICA: "Ovamboland" cult. PRE, fl. 30.iii.1951, *Schinz s.n.* comm. *Triebner* ex *Pienaar* (PRE), idem fl. iii.1957 (PRE); "Etosha Pan" cult. PRE; fl. xii.1959—i.1960, collector? comm. *Venter* ex *Lavranos* (PRE).

It is suspected that the "Etosha Pan" plant may well have originated from the same clone as the "Ovamboland" specimen and may have been subject to recording errors in cultivation, as it would be most surprising if this montane "mist belt" species of quartzite and granite soils were to occur at these localities. RHODESIA—E: Vumba Mountain, cult. Umtali sub *Plowes 3996*, fl. ii.1973, *L. C. Walter s.n.* (SRGH); Chimanimani Mtns. "The Corner", cult. Umtali, sub *Plowes 3137*, fl. 14.xii.1972, *O. West 7594* (SRGH); Chimanimani Mtns., Bundi Valley, fl. 10.iv.1967, *Plowes 2598B* (SRGH), ibid. cult. Umtali, fl. i.1968, *Plowes 2598A* (K, PRE); Mutema escarp., \pm 48 km SW of Melsetter, fl. 12.xi.1971, *Percy-Lancaster 13* (SRGH), idem cult. Umtali sub *Plowes 3876*, fl. 9.ii.1974 (SRGH).

—S: "Shumbari" Mtn., ± 40 km E of Fort Victoria, cult. Greendale, fl. 4.iv.1957, Leach 5572 (SRGH), idem cult. PRE, fl. 10.i.1958 (PRE); "Fort Victoria" cult. NBG, fl. 6.ii.1958, comm. Bulawayo Mus., 44378 in Herb. Compton (NBG); Belingwe Distr., gorge 3 km S of Mnene Miss., associated with Selaginella on decomposing granite, cult. Nelspruit, fl. ii.1966, Leach & Bullock 12864 (K); idem cult. Greendale, fl. 25.i.1972 (SRGH); ibid. on granite slope, cult. Nelspruit, fl. iii. 1966, Leach & Bullock 12863 (PRE); Emberengwa Mtn., mat-forming on steep slopes, banded ironstone, cult. Nelspruit, fl. xii.1965, Leach & Bullock 12884 (BOL, LISC, MO, SRGH), idem cult. Greendale, fl. iii.1966 (K, PRE), idem cult. Umtali, fl. ii.1973 (M); NW face, Emberengwa Mtn., robust plants cult. Greendale sub Leach 14879, fl. 1973–74, Bullock 71 (B, BR, NBG, ND, SRGH, Z); Buhwa Mtn., cult. Bulawayo, fl. 24.iii.1968, et cult. Umtali sub Plowes 3321, fl. 12.xi.1970, Bullock 189 (SRGH).

Putative hybrid: H. volkartii × ? H. hislopii. A plant which appears probably to be of this parentage has been collected on Vumba Mtn., on the eastern border of

Rhodesia, cult. Umtali sub Plowes 3997, fl. 13.i.1976, L. C. Walter s.n. (SRGH).

Plant tufted or sometimes mat-forming; *stems* erect or decumbent-erect, 5-angled (4-angled appear to be very rare), usually about 4–5 cm high.

Pedicel: 5-11 (13,5) mm long.

Sepals: narrowly ovate attenuate, 5,5-7 (8) mm \times 1,25-1,75 mm.

Corolla: campanulate with abruptly, widely spreading lobes, (20) 22–27 (30) mm across the tips of the lobes, cream to brownish coloured, scabridulous outside, inside concentrically lined and marked with dull crimson; papillae rather slender, more or less terete or flattened, up to 1,75–2,5 mm long, sometimes shortly apiculate; tube about twice as broad as long, averaging \pm 10 (exceptionally 13,5) mm diam. \times \pm 5 mm deep; lobes deltate, usually wider than long 4,5–9 mm long, 7–9,5 mm wide, usually recurved; intermediate lobes 2–2,5 mm long.

Corona: outer lobes very variable in both size and shape; inner lobes variably transversely gibbous at the base, minutely papillose at the variably clavate, often somewhat recurved, obtuse apex, sometimes slightly ventricose shortly below the apex on the inner face, then occasionally somewhat "foot-like"; tubercle below the anther wings, subacute, conical, obscuring the orifice.

Pollinia: oblong-elliptic, $0.33-0.45 \times 0.25-0.34$ mm.

b. var. repens (Lavranos) Lavranos in Jl S. Afr. Bot. 38: 43 (1972)—Jacobsen, Lexicon Succ. Pl.: 278 (1974).

Type: Moçambique, Manica e Sofala, Garuso, cult. Johannesburg, *Schweickerdt* 3469 (PRE, holo.! SRGH!).

Huernia repens Lavranos in Jl S. Afr. Bot. 27: 11 (1961)—Jacobsen, Sukk. Lexikon: 244 (1970)—Plowes in Excelsa 1: 16 (1971).

Type: as above.

Var. repens is distinguished by its long creeping stems, of which the angles are usually rounded and the tubercle teeth more or less obsolescent.

Chromosome number: 2n = 44, G. Reese u. H. Kressel (1971).

RHODESIA—E: Chipinga Distr., Smithfield Farm, ± 27 km S of Chipinga, 8.iv.1974, *Percy-Lancaster 112* (SRGH).

—S: Kyle Dam, near Fort Victoria, cult. Umtali, fl. 1967 et 1975, *Plowes 2483* (SRGH); Mangugwe Mtn., Tokwe-Mukorzi Dam, on granite in mist-belt, cult. Umtali sub *Plowes 2555*, fl. 29.iv.1967, *Buckland s.n.* (SRGH).

MOÇAMBIQUE—MS: NW slopes of Espungabera Mtn., "stems hanging, sometimes up to 1 m long", fl. 12.x.1973, *Percy-Lancaster 74* (SRGH), idem cult. Umtali sub *Plowes 4515*, fl. i.1974 (SRGH); Serra de Choa, "28 km de Vila Gouveia", cult. Sintra, Portugal, fl. 29.viii.1966, *Torre & Correia 13513* (LISC); Garuso, cult. Johannesburg, fl. 29.xii.1959, *Schweickerdt 3469* (PRE), fl. 5.v.1960 (PRE, SRGH), idem, cult. PRE, fl. ii.1959 (PRE); ibid. cult. Umtali, fl. 14.ii.1967, *Plowes 2524* (PRE).

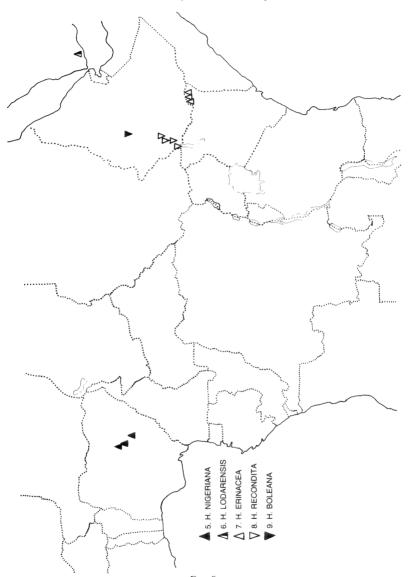


FIG. 8. Approximate areas of distribution of species of Group II.

GROUP II

5. Huernia nigeriana Lavranos in Jl S. Afr. Bot. 27: 233 (1961).

Type: Nigeria, Bauchi, cult. Johannesburg sub Lavranos 1058 (PRE, holo.!).

Huernia volkartii Gossweiler ex White & Sloane var. nigeriana (Lavranos) Lavranos in Jl S. Afr. Bot. **30:** 25 (1964)—Jacobsen, Sukk. Lexikon: 245 (1970).

Type: as above.

Huernia volkartii Werderm. & Peitsch., R. A. Dyer in Flower. Pl. Afr. 38: t. 1519B (1967), p.p. quoad ref. var. nigeriana.

Type: as above.

Huernia volkartii Gossweiler, sensu Plowes in Excelsa 1: 16 (1971), p.p. quoad distrib. Nigeria.

Huernia volkartii Werderm. & Peitsch. var. nigeriana (Lavranos) Lavranos, sensu Jacobsen, Lexicon Succ. Pl.: 277 (1974).

Chromosome number: 2n = 22, Focke Albers (1975).

NIGERIA—48 km W of Bauchi, cult. Johannesburg, 1961, sub *Lavranos 1058* (PRE); ± 5 km S of Jos, cult. PRE, *Reynolds 9623* (PRE, SRGH); Jos, cult. Kumasi, Ghana, *L. E. Newton 518* (SRGH); Pankshin, ± 128 km SE of Jos, cult. Greendale, fl. ii.1973, *L. E. Newton 1194* sub *Leach 14902* (BOL, K, PRE, SRGH). "Plants plentiful among grass and sedge tufts on rocky slope near Pankshin."

Stems: erect or decumbent-ascending, up to 8 cm long $\times \pm 1$ cm, 5-angled, with rather small (up to 2.5 mm high), very acute, spreading teeth along the angles.

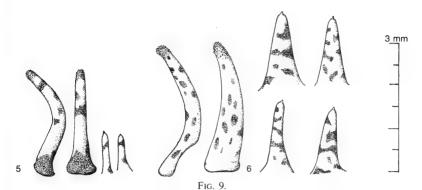
Pedicel: 8-10 mm long.

Sepals: usually 3-nerved, acuminate, 6–7 mm \times 1,25–1,75 mm.

Corolla: in bud reminiscent of that of H. loesenerana, 20–25 mm across the tips of the lobes, cream-coloured, minutely asperulate outside, sometimes almost smooth, inside marked with blood-red blotches and broken lines; papillae rather slender, narrowly conical or subterete, up to \pm 1 mm long, sometimes minutely apiculate; tube rather deeply cup-shaped, sometimes very slightly urceolate, 9–10 mm diam., 7–9 mm deep; lobes spreading, but not abruptly so, usually recurved, deltate, 6,5–7 mm long, 5,5–6,5 mm wide at the base, with a continuous, narrow, dark red, minutely denticulate, papillose margin.

Corona: inner lobes 2,5–3 mm long, incumbent on the anthers, connivent, diverging from about half-way, widened at the base but scarcely gibbous, tapering to a small, minutely papillose, obtuse apex. Nectarial orifice almost obscured by a relatively acute tubercle.

Pollinia: oblong-elliptic, $0.4-0.5 \text{ mm} \times 0.26-0.3 \text{ mm}$.



 H. nigeriana, Jos, Nigeria, Newton 1194.
 H. lodarensis, Lodar, S.W. Arabia, Lavranos 1789.

When Lavranos reduced his species to varietal rank in *H. volkartii* he appears possibly to have been unduly influenced by the apparent overall similarity of the two taxa involved; a similarity which, on critical examination of the material now available, appears to be rather superficial.

In proportionally longer tube, much shorter papillae, subulate inner coronalobes, as well as in the continuous, dark red, papillose-denticulate margin of the corolla lobes and very acute stem teeth, *H. nigeriana* is considered to be far more closely related to *H. lodarensis* Lavr., from S.W. Arabia, than to *H. volkartii*. Such a relationship also appears to be more acceptable on distributional grounds than one with the southerly based *H. hystrix* complex to which *H. volkartii* appears definitely to belong; it is also considerably strengthened by the cytological evidence, both northern species being diploid while *H. volkartii* is tetraploid. From this latter *H. nigeriana* is additionally distinguished by its less abruptly spreading corolla-lobes, less scabrid outer surface and generally more robust habit.

6. Huernia lodarensis Lavranos in Jl S. Afr. Bot. **27:** 233 (1961).—Jacobsen, Lexicon Succ. Pl.: 275 (1974).

Type: S. Arabia, Audhali Sultanate, Lodar, Lavranos 1900 (K, "spirit"!).

This species appears from the records to be known only from the vicinity of Lodar and to be represented in herbaria other than Kew by a single flower only, cult. Umtali sub *Plowes 3604*, fl. 29.xii.1973, *Lavranos 1789* (SRGH).

Stems: stout, 5-angled, with widely spreading, stout, very acute, almost subulate stem teeth.

Pedicel: 8-12 mm long.

Sepals: narrowly attenuate, 1-nerved, 8-10 mm × 1-1,5 mm.

 $Corolla: \pm 36$ mm across the tips of the lobes, cream-coloured, outside minutely asperulous, inside marked with purple-brown, often confluent blotches and broken lines; papillae stout, subconical, sometimes minutely apiculate; up to 1,5 (1,75) mm high, 0,75 (sometimes almost 1 mm) broad at the base; tube campanulate, ± 12 mm diam. \times 7,5 mm deep, sparingly asperulate inside towards the base; lobes widely spreading recurved, deltate, shortly very narrowly acuminate, 3-nerved with the central very prominent, 11 mm long, 9–9,5 mm wide, with a continuous, papillose-denticulate, rather frill-like, erect, dark purple-brown margin.

Corona: raised slightly above the base of the tube on a disc-like central platform, with the outer lobes adpressed to the base of the tube only towards their apex; inner lobes \pm 3 mm long dorsally flattened and widened towards the weakly transversely gibbous base, tapering to a small, minutely scabrous, obtuse apex.

Pollinia: oblong-elliptic, \pm 0,4 mm \times 0,25 mm.

On the presently available evidence it seems probable that all or some of the following characters, or combinations of these, will prove to be diagnostic. Long narrow sepals; short stout papillae; corona raised on a central "platform" and "subulate" inner corona-lobes; of these, those relating to the corona are possibly most important, particularly the peculiar central "platform" which I have not observed in any other species. The characteristic stems and corolla margin may also, if constant, provide at least confirmatory characters; in any event there seems no doubt that *H. lodarensis* is perfectly distinct from any of the related taxa herein discussed.

The stout papillae and subulate inner corona-lobes are both clearly to be seen in the photo by the Botanical Research Institute, Pretoria, Jl S. Afr. Bot. 27: fig. 1, Pl. XVI (1961).

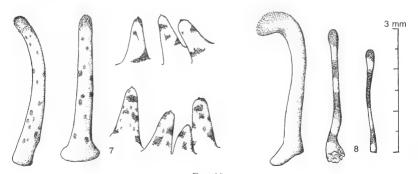


Fig. 10.
7. H. erinacea, Dandu, Kenya, Lavranos sub NBG 237/59. 8. H. recondita, Ethiopia, Gilbert s.n. sub Leach 15562.

7. Huernia erinacea Bally in Flower. Pl. Afr. **31:** t.1206 (1956).—Jacobsen, Handb. Succ. Pl. **2:** 621 (1960), et Lexicon Succ. Pl.: 273 (1974).

Type: Kenya, N.F.D., Dandu, Gillett 12629 (K; PRE!).

Chromosome number: 2n = 44, Kew (Cyt. 62–363 & 382), and Reese u. Kressel (1967).

KENYA, N.F.D.—Kenya-Ethiopia border, *Bally*, "spirit" 295–58 (K); ibid. *Gillett* "spirit" E.N. 330–52 (K); Dandu, ± 96 km E of Moyale, cult. PRE, fl. 12.v.1952, *Gillett 12629* (PRE); ibid. cult. NBG 237/59, fl. 9.ii.1962 & 29.iii.1962, *Lavranos s.n.* (NBG).

Stems: obtusely 5-angled, somewhat obsolescently tubercle-toothed, procumbent, up to 60 mm long \times 10 mm in the material seen.

Pedicel: 7-15 (20 Bally) mm long.

Sepals: narrowly ovate, acuminate, 1-nerved, 6 mm × 1,75 mm.

Corolla: 40–42 mm across the tips of the lobes, yellowish; inside marked with red-brown (blackish purple Bally) spots and lines; papillae subobtusely conical, relatively crowded, up to 1,5 mm high (0,75 Bally), 0,75 mm broad at the base, marked with dark purple; tube, shallowly urceolate, 12–15 mm diam., 7–10 mm deep (apparently somewhat variable in depth), smooth inside; tobes spreading recurved, narrowly deltate, 8–9 mm wide at the base, 15,5–17,5 mm long (13 × 20 Bally) with a continuous, irregularly denticulate-papillose (some papillae relatively large), dark purple margin.

Corona: inner lobes erect, 3,5 mm long, slightly divergent, blackish purple at the enlarged base, whitish above, minutely purple spotted, more or less terete, tapering slightly to the minutely papillose, obtuse apex (cylindric, smoothly rounded *Bally*).

Related to *H. hystrix* this tetraploid east African species differs significantly in numerous characters. In addition to its generally quite different, obtusely angled procumbent stems, the distinguishing floral characters include its much shorter pedicels and long narrow corolla-lobes (most evident in comparison of buds) with a continuous, denticulate-papillose margin and much shorter papillae which are entirely different in character from those of its southern relative, while the obtuse inner corona-lobes are "toto caelo" different. Among east African species it appears, in stem characters, to be closest to the recently described *H. recondita* although otherwise separated therefrom by many of the floral characters by which it differs from *H. hystrix*, and particularly by the entirely different papillae of the Ethiopian species; florally it is, it seems, closest to *H. lodarensis* although easily distinguished from that species by its narrowly triangular corolla lobes.

8. Huernia recondita M. G. Gilbert in Cactus Succ. J., Los Ang. **47** (1): 6 (1975).

Type: Ethiopia, Gilbert 1729 (K, holo.; ADAB; EA).

ETHIOPIA—87 km N of Arba Minch, M. G. Gilbert s.n., cult. Umtali, fl. i.1976, sub *Plowes 4261* (SRGH), idem sine loc. comm. Lavranos cult. SRGH, fl. iii.1976, sub Leach 15562 (SRGH).

According to the map supplied by its author, *H. recondita* is restricted to a relatively small area, mainly in Gemu Gofa Govenerate General, in the southwestern corner of Ethiopia.

Unfortunately I have not seen the holotype which is preserved in liquid in the herbarium at Kew, and the following notes are based on the above specimens collected by Mr. Gilbert and to some extent on the original description.

Naturally such meagre material gives little idea of any variability possessed by this taxon; one point does however emerge. By far the most distinctive character of this species lies in the extremely slender, very long papillae which attain a length of at least 2,8 mm, although in the original description this measurement is given as 1,8 mm. Since this figure occurs twice in the article concerned it seems improbable that it is an error and that the difference represents a measure of the variability to be found in this character.

Stems: procumbent, obtusely 4-angled (rarely 5–7) with obsolescent tubercle teeth, 7,5 cm long (up to 50), 1–1,25 cm diam.

Pedicel: terete, tapering to \pm 1,75 mm diam. at the apex, 17,5 mm long (25–30 mm).

Sepals: ovate acuminate, obscurely 5-nerved, obtusely keeled, \pm 10 mm \times 2 mm.

 $Corolla: \pm 42$ (34) mm across the tips of the lobes, yellowish, densely minutely papillose-asperulate on the outside of the tube, becoming sparsely so on the prominently 3 (5)-nerved lobes, the central nerve exceptionally prominent, inside marked with irregular red blotches and in the tube with transverse lines; papillae very slender, cylindric or very slightly expanding to a slightly clavate, obtuse apex, 0.125-0.2 (0,2) mm diam., up to 2.8 (1,8) mm long, red and yellow banded; tube campanulate (slightly constricted at the throat), 12.5 (10–11) mm diam., 7.5 (8–9) mm deep; lobes deltate, shortly acuminate (acute deltate), 12 (9) mm wide, 15 (12) mm long, with a narrow, dark red, continuous margin, erectly papillose-denticulate above, fleshy, subacute and entire beneath.

Corona: inner lobes \pm 3 mm long, erect, more or less terete, slightly divergent towards the recurved, slightly clavate, horizontally somewhat ovate, minutely asperulate apex, transversely slightly gibbous at the base; anther wings very prominent; nectarial orifice more or less obscured by a rather small tubercle.

Pollinia: oblong-elliptic, \pm 0,45 mm \times 0,28 - 0,3 mm.

Measurements and details in brackets are those of the original description.

While obviously belonging in the *H. hystrix-lodarensis* relationship, *H. recondita* appears to be satisfactorily distinct at specific level on the evidence of several "good" characters in addition to its red buds. Possibly most important are the long, extremely slender papillae, which are quite different from any others I have seen, and the 4-angled, subcylindric, creeping stems. The inner lobes of the corona are also of a different pattern from any of the others, although closest probably to those of *H. volkartii*; however, as very little is known regarding coronal variability in *H. recondita* this should be treated with some reserve in view of the extensive variations to be found in some members of the group. Although 5-angled, there is otherwise considerable similarity in the stem characters of *H. volkartii* var. repens.

9. Huernia boleana M. G. Gilbert in Cactus Succ. J., Los Ang., **47** (1): 10 (1975).

Type: Ethiopia, Shoa, Bole Valley, M. G. & S. B. Gilbert 2431 (ADAB; K, holo., "spirit").

H. boleana is included here as despite its distinctiveness it appears ex descr. to belong in the same overall grouping. Unfortunately I have not yet had the opportunity of examining live or spirit material but rather doubt its suggested close relationship with H. longituba of which decidedly papillose, clavate inner coronalobes are so characteristic and corolla shape so variable. In coronal characters this Ethiopian species appears to me to have more in common with some of the northerly based species such as H. lodarensis than with the southern groups. Judging from other sections of the group, it seems probable that the character of the papillae might assist in the assessment of possible relationships and from the description it seems possible that these may well belong with those of H. recondita and hence that similarities with such species as H. longituba are perhaps due to convergence rather than to a more direct relationship.

Stems: 5-angled, strongly toothed, \pm 1 cm thick, erect, up to 7 cm high or sometimes pendent.

Pedicel: 5–10 mm long.

Sepals: 6 mm long.

 $Corolla: \pm 27$ mm diam., deeply campanulate or tubular, outside smooth, inside pale cream, marked with small red dots; papillae slender, cylindric, up to 1,4 mm long, white dotted with red; $tube \pm 12$ mm diam.; lobes deltate-accuminate, usually longer than wide.

Corona: inner lobes connivent-erect becoming divergent above, ± 4 mm long, subulate, tapering to the minutely obtuse, smooth apex, with a transverse gibbosity at the base; nectarial orifice apparently obscured by a prominent subacute tubercle.

The foregoing details are compiled from the original description and figures as I have not seen a specimen.

GROUP III

10. Huernia whitesloaneana Nel in Cactus Succ. J., Los Ang., **8:** 9 (1936).—R. A. Dyer in Flower. Pl. S. Afr. **16:** t.632 (1936).—White & Sloane, Stap. ed. 2, **3:** 1172 (1937).—Luckhoff, Stap. S. Afr.: 196, 206 (1952).—Jacobsen, Handb. Succ. Pl. **2:** 631 (1960), et Lexicon Succ. Pl.: 278 (1974).

Type: S. Africa, Transvaal, Zoutpansberg, $Nel\ s.n.$ in Herb. Stellenbosch $5720\ (STE!)$.

TRANSVAAL—2229 (Waterpoort): Wyllies Poort (-DD), cult. PRE, *Hardy 384* (PRE, SRGH), cult. NBG 843/60, fl. 29.iii. 1962 (NBG); Zoutpansberg, Entabene, *G. Nel s.n.* in Herb. Stellenbosch *5720* (STE), cult. NBG, fl. 26.ii.1957, *A. W. Riley s.n.* (NBG), cult. PRE, fl. iv.1936, *Taylor 2514* (PRE).

—2328 (Maasstroom): Blaauwberg, Mohlakeng Plateau, (-BB), fl. 12.i.1955, Codd & Dyer 9111 (PRE).

—2329 (Pietersburg): Zoutpansberg, Mountain Inn (-BB), cult. Umtali, fl. 6.xi.1968, *Plowes 2617* (PRE), fl. 9.iii.1974 (SRGH).

Plant: small, tufted, usually less than 5 cm high.

Stems: 4/5-angled, prominently dentate, deeply sulcate.

Pedicel: 5 (8) mm long.

Sepals: ovate-acuminate, 5-nerved, the central forming a very prominent obtuse keel, $5-7 \text{ mm} \times 2 \text{ mm}$.

Corolla: campanulate, \pm 14 mm diam., 14,5 mm long, outside smooth, purplish mottled; inside irregularly spotted and concentrically lined with purplish red; papillae \pm conical, occasionally slightly flattened, up to 1,25 mm long, very shortly minutely apiculate; tube 8–10 mm long, \pm 12 mm diam., smooth inside; lobes deltate, \pm 6 mm \times 6 mm, erect or suberect.

Corona: outer lobes more or less transversely narrowly oblong with the outer margin shallowly incurved, thickened and fused (intergrown) with the base of the tube at its centre; inner lobes subulate, \pm 3 mm long, dorsiventrally compressed towards the transversely gibbous base, nearly 1 mm wide, convergent above becoming divergent from about half way, tapering to the small (\pm 0,2 mm diam.), sometimes very slightly enlarged, obtuse, minutely papillose apex; nectarial orifice partially obscured by a rather prominent obtuse tubercle.

Pollinia: 0,33-0,4 mm × 0,22-0,26 mm.

This very distinctive, small flowered species is restricted, as far as is known, to a small, relatively high rainfall area of the northern Transvaal on the upper slopes of the Zoutpansberg and Blaauwberg.

In corolla shape it seems probably to be closest to *H. loesenerana*, but in other features approaches more closely perhaps to *H. hislopii*, while the most unusual fusing of the centre portion of the outer margin of the outer corona-lobe with the base of the tube is believed to be peculiar to this species.

11. Huernia occulta Leach & Plowes in Jl S. Afr. Bot. **32** (1): 57 (1966).— Jacobsen, Sukk. Lexikon: 276 (1970), et Lexicon Succ. Pl.: 244 (1974).—Plowes in Excelsa **1:** 16 (1971).

Huernia hislopii sensu White & Sloane, Stap. ed. 2, 3: 945 (1937), p.p.—sensu Phillips in Flower. Pl. S. Afr. 19: t.758 (1939).

Type: Rhodesia, near Zimbabwe, Leach 11661 (K, PRE, SRGH, holo.).

Chromosome number: 2n = 22, Focke Albers (1974, 1975).

With a scattered distribution on the granite hills of the southern escarpment area of Rhodesia this endemic species appears to be quite rare. However, it seems quite possible that its rarity may be more apparent than real as seemingly eminently suitable habitats abound in this area and it is considered that the relative paucity of records may be due more to its effective concealment among the grass tussocks of its habitat than to its rarity. Although a few gatherings have been made since this species was published these do not represent any significant extension of its distribution as then recorded.

Plants: usually creeping among grasses, then almost or quite completely concealed.

Stems: slender, 5-angled, deeply sulcate.

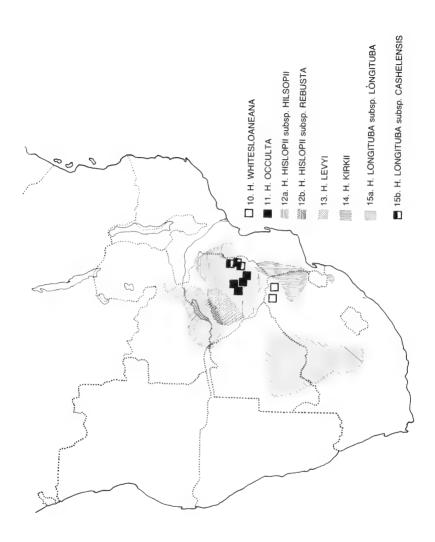
Pedicel: 12-24 mm long.

Sepals: narrowly ovate-acuminate, 6-8 mm × 1,5 mm.

Corolla: cream-coloured, bicampanulate, with a broad spreading limb about 22,5 mm diam., usually slightly scabridulous outside low down, inside irregularly marked with tawny red blotches; papillae short, conical or obtusely conical, up to \pm 1 mm high; tube more or less cylindric, usually \pm 10 mm diam., somewhat variable in length, entirely shining dark purple inside; lobes deltate, shortly acuminate, sub-erect or spreading, \pm as long as broad, with a minutely tuberculate margin.

Corona: inner lobes \pm 3,5 mm long, subterete, much broadened towards the base, sometimes rather obscurely transversely gibbous, tapering rather sharply to the small, obtuse, sometimes very slightly enlarged, sometimes shortly recurved, minutely obtusely tuberculate or minutely rugulose apex, with their base low down on the staminal column, often almost touching the corona disc; nectarial orifice rather large, partially or completely obscured by a prominent obtuse tubercle.

Pollinia: oblong-elliptic, 0,38–0,4 mm \times 0,26–0,3 mm.



 $\label{eq:Fig.11.} Fig.~11.$ Approximate areas of distribution of species of Group III.

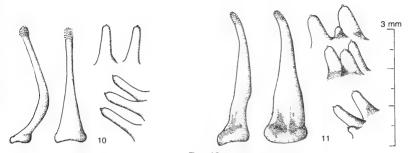


Fig. 12. 10. H. whitesloaneana, Zoutpansberg, Transvaal, Plowes 2617. 11. H. occulta, Zimbabwe, Rhodesia, Leach 11661.

During its early history this handsome species was somewhat unaccountably confused with the frequently associated but quite distinct *H. hislopii*, which is relatively common in Rhodesia and a small area of Moçambique. Comparisons of the brief descriptions provided will disclose a number of diagnostic characters; of these possibly the most significant is that the inner corona-lobes originate near the base of the staminal column, as opposed to their more usual position near its apex. Apart from the slender, fluted stems the species is, of course, easily recognized also by its handsome bicampanulate flowers with the inside of the more or less cylindric tube shining dark purple in contrast to the concentrically red-lined globose inflated tube of *H. hislopii*. In bicampanulate flowers, unicoloured tube and corolla markings *H. occulta* approaches *H. kirkii*, but its affinity with that species is considered to be less close than with the frequently closely associated *H. hislopii*.

12. Huernia hislopii Turrill in Kew Bull. 1922: 30 (1922).—White & Sloane, Stapelieae ed. 2, 3: 944 (1937), p.p.—Luckhoff, Stapelieae S. Afr.: 224 (1952), p.p.—Jacobsen, Handb. Succ. Pl. 2: 622 (1960), p.p. et Lexicon Succ. Pl.: 274 (1974).—Leach & Plowes in Jl S. Afr. Bot. 32 (1): 51–57 (1966).—Plowes in Excelsa 1: 15 (1971).

Type: Rhodesia, A. Hislop, cult. Kew No. 191 (K!).

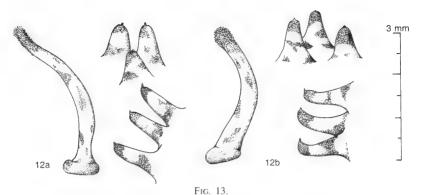
· *H. kirkii* sensu White & Sloane, tom. cit.: 942 (1937), p.p.—Jacobsen, tom. cit.: 623 (1960), p.p.

H. scabra sensu Markgraf in Trans. Rhod. Sci. Ass. 43: 128 (1951).

Two subspecies are recognized.

a. subsp. hislopii

Chromosome number: 2n = 22, Kelly: 189 in Leach (1970); 2n = 33, 2n = 44, Reese (1971).



12a. H. hislopii subsp. hislopii, Umtali, Rhodesia, Leach 5698. 12b. H. hislopii subsp. robusta, Gokwe, Rhodesia, Bingham 874.

The typical subspecies is distributed almost throughout Rhodesia, where it is probably the commonest stapeliad, with an extension into a small area of Moçambique in the Manica e Sofala District, adjacent to the Rhodesian border. Plants occur almost exclusively on the granite hills and outcrops of the main watershed and escarpment areas.

The following recent gatherings slightly extend the known distribution of this taxon.

RHODESIA—N: Bindura, Paradise Pools, cult. Umtali sub *Plowes 2567*, fl 3.i.1967, *O. West s.n.* (SRGH).

—W: ± 12 km S of Plumtree, Ingwezi River, cult. Umtali sub *Plowes 4003*, fl. 9.ii.1973, *G. H. Brewer s.n.* (SRGH).

—S: Gona-re-Zhou, Marhumbini Mission, cult. Greendale sub *Leach 14235*, fl. ii.1970, *Blake 117* (SRGH).

Subsp. hislopii has sometimes, in the past, been confused with both H. kirkii and H. occulta; apart from the fact that both of these bear bicampanulate flowers, subsp. hislopii may be immediately recognized by its distinctly concentrically lined and conspicuously globose-inflated tube (in contrast to the unicoloured blackish-maroon tube of both relatives) and additionally from the former by its subulate inner corona-lobes and quite different, much stouter papillae, and from the latter by its much taller corona and relatively stout stems.

Plants: tufted, usually growing along cracks and in crevices on granite rocks, or occasionally forming clumps on deeper soil.

Stems: 5-angled, strongly toothed.

Pedicel: 6-20 mm long.

Sepals: narrowly ovate-attenuate, 6–10 mm \times 1,75–2 mm.

Corolla: cream-coloured, smooth outside, 45–57 mm diam.; inside marked with brown-red to maroon blotches on a whitish to creamy ground colour, distinctly transversely red-lined within the tube; papillae stout, up to 1 mm high, somewhat compressed and broadened to \pm 0,75 mm near the base, obtuse, usually very shortly mucronate; $tube \pm 11$ –15 mm in diam. and length, conspicuously globose-inflated at the base, rather sharply constricted at the throat; lobes widely, usually abruptly spreading and often recurved, deltate-acuminate, sometimes almost deltate-caudate, longer than wide, 15–22 mm long \times 12–18 mm wide.

Corona: inner lobes 4–4,5 mm long, transversely gibbous at the base, subulate, at first convergent, becoming divergent from a little below half-way, obtuse at the minutely papillose apex; nectarial orifice almost completely concealed by a scarcely prominent tubercle.

Pollinia: elliptic-oblong, $0,4-0,45 \times 0,28-0,3$ mm.

b. subsp. **robusta** Leach & Plowes in Jl S. Afr. Bot. **32** (1): 53 (1966).— Jacobsen, Lexicon Succ. Pl.: 274 (1974).

Type: Rhodesia, Lupani Distr., *Leach 11628* (BM, G, K, LISC, SRGH, holo.). Chromosome number: 2n = 44, Focke Albers (1975).

It is this subspecies which has been the more consistently confused with *H. kirkii*, probably on account of its more nearly unicoloured, somewhat less globose tube; however, it is easily distinguished from that bicampanulate flowered species, especially in live specimens, by its 5/7-angled stems, its longer, campanulate corolla with shorter, stouter, minutely mucronate, mottled papillae and its subulate inner corona-lobes which are less prominently papillose and not at all or scarcely enlarged at the obtuse apex (in dry material these sometimes appear to be slightly subclavate due to unequal shrinkage but never to the extent of those of *H. kirkii*).

Subsp. *robusta* is equally easily distinguished from the typical subspecies by its more robust 5/7-angled stems, more or less unicoloured (distinctly transversely lined in subsp. *hislopii*), less globose, longer tube, and proportionally shorter, scarcely acuminate corolla-lobes, as well as by its more robust inner corona-lobes.

Plants occur mainly on sandy or gravelly soils in the thorn bush and *mopane* woodland of western Rhodesia.

The known distribution of this subspecies is slightly extended by the following records of recent gatherings.

RHODESIA—N: Charama plateau, south of Sengwa River, Gokwe Distr., Simon 407 (SRGH).

—W: near Robins Camp, Wankie Nat. Park, cult. "Ewanrigg", fl. 23.iii.1973, *Buckland s.n.* (SRGH).

—C: Sebakwe Dam, Que Que, cult. Umtali sub *Plowes 4084*, fl. i. 1973, *Blake 104* (SRGH); "Quetanga", 24 km E of Que Que, cult. Umtali sub *Plowes 3294*, D. T. Crow s.n. (K).

It is interesting to note that the distribution of this subspecies is associated with initially westward flowing tributaries of the Zambesi and not at all with those of the Sabi, Lundi and Limpopo systems.

13. Huernia levyi Oberm. in Flower. Pl. S. Afr. **16:** t.616 (1936).—White & Sloane, Stap. ed. 2, **3:** 936 (1937).—Luckhoff, Stap. S. Afr.: 195, 218 (1952).—Jacobsen, Handb. Succ. Pl. **2:** 624 (1960), et Sukk. Lexikon: 243 (1970), et Lexicon Succ. Pl.: 275 (1974).—Plowes in Excelsa **1:** 16 (1971).

Type: Rhodesia, Wankie, B. Levy in Herb. Transv. Mus. 31142 (PRE!). Chromosome number: 2n = 22, Focke Albers (1976).

CAPRIVI STRIP—Mpilila Island, fl. Jan. 1959, *Killick & Leistner 3403* (PRE). ZAMBIA—S: Kafue Nat. Park, Shibatwa Riv., Hort. Plowes., Umtali, fl. Nov. 1967, *Mitchell 3006/3* (SRGH), ibid. fl. Feb. 1971; *Mitchell 3006/2* (K, PRE); Namwala, Hort. Leach., Nelspruit, fl. Jan. 1966, *Mitchell 3005* (BOL; SRGH); Livingstone Distr., Songwe Riv. Gorge, Hort. Plowes., Umtali, & SRGH Salisbury, *Mitchell 3013* (K, PRE); Candelabra Pool, Victoria Falls, cult. Greendale, fl. May, 1960, *Leach 9952* (SRGH); Mazabuka Distr., Sikalongo, nr. Choma, cult. Stellenbosch, fl. Mar. 1935 & Dec. 1936, *F. Porter* sub STE *6407* (BOL); Mazabuka, cult. Greendale, fl. Feb. 1960, *Leach 9796* (SRGH) et fl. Feb. 1961, *Leach 10592* (SRGH).

—E: Road to Chipata, \pm 215 km E of Lusaka, cult. Salisbury, fl. 1973–75, Anton-Smith sub Leach 14801 (BOL, BR, K, MO, PRE, SRGH).

—C: "40 mls from Broken Hill" Feb. 1928, comm. Tapscott in Herb. Bolus. 31304 and 31305 (BOL).

RHODESIA—W: Wankie, cult. Pretoria, fl. Apr. 1932, *B. Levy* in Herb. Transv. Mus. *31142* (PRE), idem in Nat. Herb. *19602* (PRE), idem, Hort. van Balen., fl. Feb. 1935 (PRE) cult. Stellenbosch, fl. Jan. 1935, in STE *6468* (BOL); ibid. cult. Salisbury, fl. Feb. 1934, *Eyles 8360* (SRGH), fl. Jan. 1936, *Eyles 8532* (SRGH); Inyantui, cult. Greendale, fl. May 1960, *Leach 9974* (BOL, K, SRGH).

—N: Zambesi/Sebungwe Junction, cult. Bulawayo Mus., M. Paterson 12 (SRGH); Gokwe, fl. Oct, 1963, Bingham 877 (SRGH); ibid., cult. Salisbury, fl. Nov. 1971, Kimberley & Pienaar 1 (SRGH); Kariba, Sanyati Riv., cult. Bulawayo Mus., M. Paterson 129 (PRE); Kariba Gorge, cult. NBG 705/56, fl. Feb. 1957, Smithers s.n. (NBG); Kariba Dam, cult. PRE, fl. Dec. 1959, Hardy in PRE 13797 (PRE); "Near Kariba", cult. Greendale, fl. Feb. 1961, Goldsmith sub Leach 10589 (SRGH); Mangula, fl. Dec. 1975, Percy-Lancaster 141 (K; SRGH).

Plant: stoutly tufted.

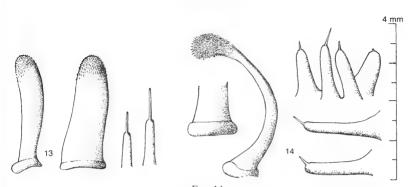


Fig. 14.

13. H. levyi, 215 km E of Lusaka, Zambia, Anton-Smith s.n. 14. H. kirkii, Mabalane, Moçambique, Leach & Bayliss 11775.

Stems: 4/5-angled, strongly toothed, usually \pm 2,5 cm or more thick.

Pedicel: 4-8 mm long.

Sepals: ovate-acuminate, prominently 1-nerved, \pm 9 mm \times 2,5 mm.

Corolla: tubular-campanulate, outside brownish, prominently nerved and scabrous, inside dark maroon becoming yellowish on the lobes with dark red blotches; $tube \pm 30$ mm long, sparsely minutely asperulate at the lightly excavated basal portion with a densely minutely papillose, raised annulus ± 4 mm above the base, densely papillose above the annulus; papillae dark maroon, narrowly elongated conical, obtuse, up to 1,25 mm long, bearing setae \pm as long as the papillae, becoming reduced above and on the lobes and lacking setae; lobes suberect to spreading, relatively short, deltate, shortly acuminate, $\pm 7-12$ mm broad at the base, $\pm 7-10$ mm long.

Corona: outer lobes much reduced to form a somewhat crenate or almost circular disc; inner lobes erect, stout, somewhat transversely gibbous at the base, dorsiventrally slightly compressed, slightly subclavate seen from the side, \pm 3 mm long, 1 mm wide \times 0,6 mm thick, densely minutely tuberculate towards and at the obtuse apex; nectarial orifice obscured by a very broad obtuse tubercle.

Pollinia: elliptic-oblong, 0,46 × 0,28 mm.

This immediately recognisable species, which has by far the longest tube in the genus, appears probably to be most closely related to those forms of *H. hislopii* subsp. *robusta* which occur in the Gokwe area. In these the tube is dark maroon in colour, with a somewhat similar lightly excavated basal portion, and is usually considerably elongated, while the relatively stout inner corona-lobes are to some extent reminiscent of those of *H. levyi*. However, in most respects the two taxa are obviously different and their correct identification should present no problem.

Recorded only from localities situated more or less along the Zambesi and Kafue valleys, *H. levyi* has a relatively restricted distribution. The most westerly known record is from Mpilila Island in the Caprivi Strip and the most easterly from about 215 km east of Lusaka on the Great East Road in Zambia and at just about the same longitude near Mangula in Rhodesia.

14. Huernia kirkii N.E.Br., Fl. Cap. **4** (1): 920 (1909).—Berger, Stap. u. Klein.: 170 (1910).—White & Sloane, Stapelieae ed. 2, **3**: 942 (1937), p.p.—Jacobsen, Handb. Succ. Pl. **2**: 623 (1960), p.p., et Lexicon Succ. Pl.: 274 (1974).—Leach & Plowes in Jl S. Afr. Bot. **32** (1): 43 (1966).—Plowes in Excelsa **1**: 15 (1971).—Non Phillips in Flower. Pl. S. Afr. **12**: t.442 (1932).

Type: S. Africa, Transvaal, Komatipoort, J. W. C. Kirk s.n. (K, holo!).

Huernia bicampanulata Verdoorn in Flower. Pl. S. Afr. 12: t.449 (1932).—White & Sloane, tom. cit.: 941 (1937).—Luckhoff, Stapelieae S. Afr.: 219 (1952).—Jacobsen, tom. cit.: 618 (1960).—Non Bremek. & Oberm. in Ann. Transv. Mus. 16: 429 (1935).

Type: S. Africa, Transvaal, Pietersburg Distr., G. van Son s.n. in Nat. Herb. 10136 (PRE, holo.!).

Chromosome number: 2n = 22, G. Reese (1971).

Some recent records extend the known distribution of this species in the Transvaal and into the south-eastern corner of Rhodesia, where it was not previously known to occur.

RHODESIA—S: Nuanetsi Riv., near the Moçambique border, *Walter 2897* (SRGH), ibid. cult. Umtali, fl. 25.iv.1969 sub *Plowes 3293* (SRGH); Clarendon Cliffs, "on sandstone, alt. ± 1 000 ft.", cult. Umtali sub *Plowes 2623*, 1971–73, *Liversedge s.n.* (BOL, K, PRE, SRGH), idem cult. Ewanrigg (LISC).

S. AFRICA. TRANSVAAL—2429 (Zebediela): Olifants Riv., ± 45 km E of Bewaarskloof, cult. PRE, 27.x.1970, *Hardy 3556* (PRE).

—2430 (Pilgrim's Rest): \pm 40 km NW of Burgersfort (-AC), 20.iii.1966, *Leach & Jones 13255* (BOL, K, LISC, PRE, SRGH); Gravelotte (-BB), *Percy-Lancaster 130* (SRGH).

Putative hybrid: a specimen collected near Mica (2430 BB), cult. PRE and Nelspruit, appears to be a hybrid with *H. hystrix* the other parent, *Hardy 925* (PRE, SRGH).

H. kirkii is a low altitude species of rather scattered occurrence; its erstwhile appearance of extreme rarity was due to a large extent to its confusion with H. hislopii and the erection of the synonymous H. bicampanulata. However, even now that its identity has been established, the combined records indicate that the species is by no means common.

Plants: tufted, often forming large clumps, solitary or sometimes forming small populations which are very variable as to corolla shape, colour and markings.

Stems: 4/5-angled, strongly toothed.

Pedicel: very variable in length from 12 mm to 35 mm.

Sepals: ovate-acuminate, usually prominently keeled, occasionally obtuse beneath, $5{\text -}10~\text{mm} \times 2{\text -}2{\text ,}5~\text{mm}.$

Corolla: bicampanulate, 30–50 mm diam., yellowish, outside smooth or sometimes very slightly scabridulous; inside marked with variably sized, red or maroon spots and blotches, unicoloured blackish maroon within the tube; papillae up to 2 mm high, unicoloured blackish maroon, more or less conical, usually \pm 0,5 (0,75) mm diam. at the base, obtuse, usually tipped with a short, acute bristle; tube smooth inside, rather variable in shape, often more or less pentagonal, sometimes slightly ampliate at the base and slightly constricted at the mouth, usually relatively shallow; corolla-lobes deltate-acuminate, wider than long, usually \pm 8–10 mm long \times 11–15 mm wide, erect to erectly spreading.

Corona: inner lobes usually unicoloured blackish maroon, transversely gibbous at the 1,25 mm wide base, somewhat dorsiventrally compressed, at first convergent, becoming divergent from about half-way, tapering slightly to the clavate, densely, acutely papillose apex, \pm 4,5 mm long; nectarial orifice only partially concealed by a relatively small, broadly obtuse tubercle.

Pollinia: oblong-elliptic, $0,4-0,5 \text{ mm} \times 0,23-0,3 \text{ mm}$.

15. Huernia longituba N.E.Br., Flora Cap. **4** (1): 912 (1909).—Berger, Stap. u. Klein.: 171 (1910).—Phillips in Flower. Pl. S. Afr. **10:** t.380 (1930).—White & Sloane, Stapelieae, ed. 2, **3:** 939 (1937).—Luckhoff, Stap. S. Afr.: 218 (1952).—Jacobsen, Handb. Succ. Pl. **2:** 625 (1960) et Lexicon Succ. Pl.: 275 (1974).—Leach & Plowes in Jl S. Afr. Bot. **32** (1): 45 (1966).

Type: S. Africa, Cape Province, near Douglas, *Pillans 609* (BOL! GRA!). *Huernia bicampanulata* sensu Bremek. & Oberm. in Ann. Transv. Mus. **16:** 429 (1935).

In stems, coronal characters and papillae *H. longituba* appears possibly to be most closely related to *H. kirkii* although differing widely therefrom in corolla shape and markings. In these latter there appears to be a link with the otherwise quite different *H. hislopii*, with the disjunct *H. longituba* subsp. *cashelensis* perhaps to some extent occupying a morphologically slightly intermediate position.

a. subsp. longituba

Chromosome number: 2n = 22, Focke Albers (1975).

With its main distributional area lying in southern Botswana and extending

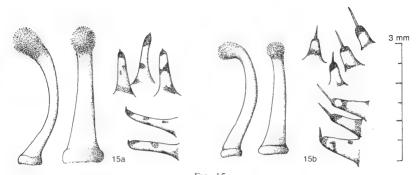


Fig. 15.

15a. H. longituba subsp. longituba, Matebe, Botswana, Smithers s.n. 15b. H. longituba subsp. cashelensis, Biriwiri, Rhodesia, Percy-Lancaster 10.

southward through the northern Cape and extreme west of the Transvaal and Orange Free State, the typical subspecies is found generally in semi-desert areas, often in the semi-shade of thorn scrub.

Plants: small, tufted, usually comprising only a few stems.

Stems: 4/5-angled, usually rather angular.

Pedicel: 4-18 mm long.

Sepals: narrowly ovate-acuminate, prominently ribbed, 7–9,5 mm \times 1,5–2,5 mm.

Corolla: tubular-campanulate, very variable in length and breadth, cream-coloured, smooth outside, or occasionally very minutely sparingly scabridulous; inside marked with brown-red to maroon spots and broken transverse lines inside the tube towards the base; papillae slender, conical, up to 1,5 mm high, mostly tipped with a minute acute mucro; tube smooth with a whitish ground colour within; lobes deltate-acute, \pm 8–10 mm long and broad, erectly to widely spreading, or rarely, strongly recurved.

Corona: inner lobes clavate, acutely papillose towards and at the apex, dorsiventrally somewhat compressed, transversely gibbous at the 1 mm wide base; nectarial orifice partially concealed by a scarcely prominent tubercle.

Pollinia: elliptic-oblong, $0.38-0.42 \text{ mm} \times 0.25-0.27 \text{ mm}$.

b. subsp. cashelensis Leach & Plowes in Jl S. Afr. Bot. 32 (1): 49 (1966).—Plowes in Excelsa 1: 16 (1971).—Jacobsen, Lexicon Succ. Pl.: 275 (1974).

Type: Rhodesia, Cashel, Leach 5404 (K, PRE, holo., SRGH).

Chromosome number: 2n = 22, Focke Albers (1975).

Subsp. *cashelensis* differs from the typical subspecies in its 5/6-angled stems, frequently slightly ampliate tube, and most characteristically in its bristle-tipped papillae, with the bristles often as long as the papillae (in this reminiscent of *H. levyi*). This subspecies is extremely variable in corolla length and breadth and particularly in the extent to which the inner corona-lobes are clavate, recurved and apically papillose.

Originally known only from the Cashel-Mutambara area this taxon is now known to be rather more widely distributed; the most northerly record is about 40 km SE of Umtali and the most southerly some 20 km W of Chipinga, near the Tanganda River. The range of habitats is also considerably extended, with plants at the new northern locality growing on granite in *Brachystegia* woodland; on dolerite at Biriwiri and the Tanganda River site, and on the stony gravelly soils of the mixed woodland localities in the Cashel area. Some recent records follow.

RHODESIA—E: "On granite in *Brachystegia* woodland", Chitora Farm, ± 15 km E of Banti Forest, cult. SRGH, *S. Mavi 605* (K, PRE, SRGH); "Chitora", ± 40 km SE of Umtali, cult. Umtali sub *Plowes 4082*, fl. 1.i.1976, *Blake 69* (SRGH); Mhakwe, Muwushu Res., Melsetter Distr., "on dolerite", cult. Umtali, fl. 26.ix.1968, *Plowes 2558* (BOL, K, PRE, SRGH); Biriwiri, on dolerite, fl. 30.x.1971, *Percy-Lancaster 10* (SRGH), ibid. cult. Umtali, fl. 12.i.1976, *Plowes 4227* (NBG, PRE), ibid, cult. Salisbury, fl. xi.1971, *Kimberley 2* (SRGH); ± 20 km W of Chipinga, "New Years Gift", "on dolerite scree", Tanganda Riv., cult. Umtali, *Plowes 3120A* (LISC, SRGH).

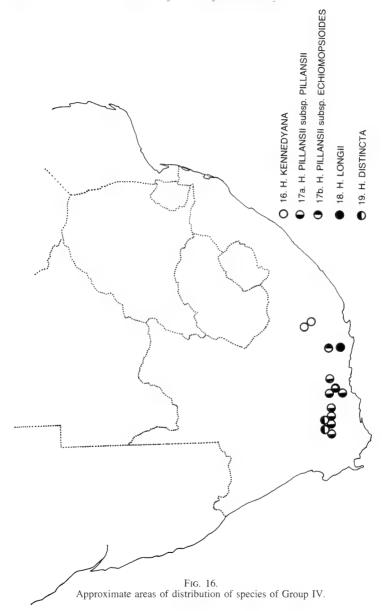
Putative hybrids with *H. verekeri* Stent the other parent are not uncommon in the Cashel and Biriwiri areas.

GROUP IV

The "pillansii-kennedyana" group

The taxa included in this most distinctive group of Karoo species are among the most remarkable in the genus and are united mainly by their multi-angular, tessellate, rather than tuberculate stems, those of the well-known typical subspecies of *H. pillansii* providing the most odd example; however, when shorn of their soft bristles by age or other causes, as they sometimes are, these can be seen to be not so very dissimilar from those of subsp. *echidnopsioides*. *H. pillansii* and *H. longii* are obviously the most closely related in floral characters although easily distinguished by their respective coronas; *H. distincta* is considered possibly to be of hybrid origin, with *H. pillansii* one parent, while *H. kennedyana* appears to be the most widely differentiated of the group, with its immediate affinities somewhat less clear.

16. Huernia kennedyana Lavranos in Jl S. Afr. Bot. **31:** 313 (1965)—Jacobsen, Lexicon Succ. Pl.: 274 (1974).



Type: S. Africa, Cradock, *Kennedy* sub *Lavranos* 2356 (PRE!). *Huernia* sp., White & Sloane, Stapelieae, ed. 2, 1: 60 (1937).

S. AFRICA. CAPE—3225 (Somerset East): "Welbedagt", ± 16 km W of Cradock (-AB), comm. *Kennedy*, cult. Johannesburg sub *Lavranos 2356* (PRE), idem cult. Umtali sub *Plowes 3275* (SRGH), idem cult. Nelspruit sub *Leach 12818E* (SRGH); Halesowen (-BC), cult. NBG 727/31, fl. iii.1932, *H. W. James s.n.* (BOL), ibid, fl. only, iv.1932, "corolla pale purple" (Pillans), *H. W. James s.n.*, in Herb. Bolus, *31303* (BOL), idem stems only, vi.1932, *H. W. James s.n.* (BOL).

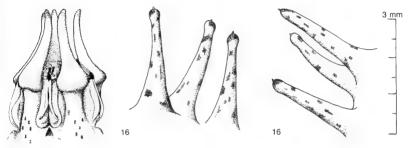


Fig. 17. 16. H. kennedyana, Cradock, Cape Province, Kennedy s.n.

It is surprising that this most distinctive species, which was in cultivation at Kirstenbosch as far back as 1931 and recognised as new by N. S. Pillans when plants flowered early in 1932, should have remained undescribed until 1965. In recent years the species appears to have been known only from the type locality, where plants with cream-coloured flowers with red-brown markings occur. However, among the plants discovered by the late Mr H. W. James, on a mountain top near Halesowen, to the south of Cradock, two distinct colour forms are found: one in which the corolla is pale purple and the other, rather more similar to the typical, in which this is dull yellow with dark purple markings. The "yellow" papillae of both these forms also appear to be somewhat differently coloured from those of specimens from the type locality.

Plants: dwarf, caespitose.

Stems: 6-8 (10)-angled, short, stout, almost globose, tessellate rather than tuberculate.

Pedicel: 4-9 (15) mm long.

Sepals: ovate-acuminate, pusticulate-scabrous, 3-4 mm × 1,75 mm.

Corolla: 20-22 mm diam., obscurely scabridulous, buff to pinkish cream

outside, inside cream or dull yellow, transversely marked with red-brown or dark purple spots and broken lines or more rarely, wholly pale purple; *papillae* terete, tapering to the obtuse, often subclavate apex, whitish or yellow, up to 2,5 (3) mm long; *tube* campanulate or hemi-spherical, 9–10 mm diam., ± 5,5 mm deep, sparingly, minutely asperulate inside towards the base; *lobes* deltate, 6–7 mm long, 6–6,5 mm wide with a subcontinuous, erect, papillose margin, 5-nerved with the central very prominent.

Corona: free, not adnate to the base of the tube; inner lobes \pm 2 mm long, subulate, broad and gibbous at the base, dorsiventrally compressed, tapering to the small, minutely papillose, obtuse, sometimes slightly enlarged apex; nectarial orifice obtusely triangular, fully exposed, the accompanying tubercle being very much reduced and somewhat distant or sometimes absent.

Pollinia: oblong-elliptic, \pm 0,39 mm \times 0,3 mm.

Huernia kennedyana may at once be recognised, even when sterile, by its stumpy, almost globose, tessellate stems, and is equally distinctive in its floral characters, of which the unique papillae are perhaps the most striking, while the short subulate inner corona-lobes, which are nearest perhaps to those of H. longii, together with the fully accessible nectarial orifice and the extreme reduction of its attendant tubercle are equally diagnostic; the combination of short, broad, scabrous sepals and broad, relatively shallow tube which is asperulate towards its base inside is also diagnostically significant.

17. Huernia pillansii N.E.Br. in Gard. Chron. 35: 50 (1904) et Flora Cap. 4 (1): 909 (1909).—Berger, Stap. u. Klein.: 168 (1910).—Marloth, Flora S. Afr. 3 (1): 95, t.22m (1932).—White & Sloane, Stapelieae, ed. 2, 3: 957 (1937).—R. A. Dyer in Flower. Pl. S. Afr. 22: t.843 (1942).—Luckhoff, Stapelieae S. Afr.: 223 (1952).—Jacobsen, Handb. Succ. Pl. 2: 627 (1960) et Lexicon Succ. Pl.: 276 (1974).—Leach in Jl S. Afr. Bot. 34 (3): 140 (1968).

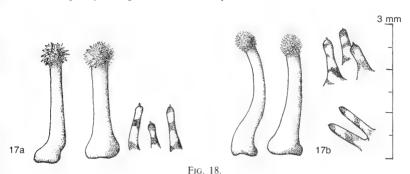
In this well-known Karoo species two subspecies are recognised, these being separated mainly by their vegetative characters.

a. subsp. pillansii

Type: S. Africa, Cape, Matjiesfontein, *Pillans 23* (BOL!, GRA!, K!). Chromosome number: 2n = 22, Focke Albers (1975).

Distribution of the typical subspecies lies entirely, as far as is known, between 33°S and 34°S, and extends from near Montagu and Matjiesfontein in the west to near Steytlerville in the east. The main concentration appears to be in the Oudtshoorn District where it is recorded from as far south as Zebra Siding between Oudtshoorn and George.

Stems: more or less cylindric, obtuse or often narrowly ovoid, densely covered with small tubercles with a decurved soft bristle at their apex, usually vertically, or sometimes spirally arranged in 14–24 closely set rows.



17a. H. pillansii subsp. pillansii, Oudtshoorn, Cape Province, Miss Schnettler s.n. 17b. H. pillansii subsp. echidnopsioides, Bayiaans Kloof, Leach & Bayliss 13612.

Pedicel: 2-8 mm long.

Sepals: narrowly ovate, attenuate, $8,5-12,5 \text{ mm} \times 1-1,25 \text{ mm}$.

Corolla: 36–48 mm diam., yellowish, smooth outside, inside densely papillose and covered in small red spots, the spots arranged in a labyrinthine pattern in the tube; papillae cylindric, \pm 0,2 mm diam., red banded and tipped, sometimes slightly subclavate, occasionally tipped with a very minute hair, up to \pm 1 (very rarely 1,5) mm high; tube campanulate, \pm 9 mm diam., 7–8,5 mm deep, smooth inside; lobes abruptly spreading, narrowly deltate-acuminate, (14) 16–20 mm long, 7–8 mm wide, 3-nerved with the nerves scarcely prominent.

Corona: free, not adnate to the base of the tube; inner lobes erect, often closely connivent or sometimes divergent towards the apex, dorsiventrally compressed and flattened, usually gibbous at the \pm 0,75 mm wide base, 2–2,5 mm long, tapering slightly to the very prominently and acutely papillose, clavate, usually knob-like apex; nectarial orifice completely or almost obscured by a prominent tubercle.

Pollinia: elliptic-oblong, 0,33–0,35 mm × 0,23 mm.

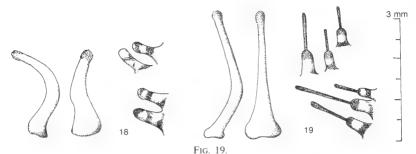
b. subsp. **echidnopsioides** Leach in Jl S. Afr. Bot. **34** (3): 140 (1968).—Jacobsen, Lexicon Succ. Pl.: 276 (1974).

Type: S. Africa, Humansdorp Distr., Baviaans Kloof, Leach & Bayliss 13612 (K!, PRE, holo.!, SRGH!).

Chromosome number: 2n = 22, Focke Albers (1976).

This subspecies, with a distribution apparently restricted to the eastern end of

Baviaan's Kloof, differs from the typical subspecies in the characters discussed in detail below.



18. H. longii, cult. specimen. 19. H. distincta, Ladismith, Cape Province, Joubert s.n.

Plants: tufted, or sometimes developing a rhizomatose habit.

Stems: usually erect, more or less terete, sometimes tapering very slightly towards the obtuse apex, \pm 1 cm diam., up to 16 cm long, with 8–10 (usually 9), vertically, or sometimes somewhat spirally arranged, closely set rows of tessellate tubercles, sharply sulcate between the rows; tubercles 1–2 mm high, each tipped with a spreading, usually slightly deflexed, acute tooth (modified leaf) becoming obsolescent with age.

Corolla: similar to that of subsp. pillansii but sparingly asperulate towards the base of the tube inside; with proportionally shorter more nearly deltate corollalobes \pm 7,5–10 mm long \times 6–8 mm wide.

18. Huernia longii Pillans in Jl S. Afr. Bot. 5: 65 (1939).

Type: S. Africa, Uitenhage Distr., Long 1154 (BOL!).

S. AFRICA. CAPE—3325 (Port Elizabeth): Groendal (-CD), cult. Port Elizabeth, sub *Pringle s.n.*, fl. iv.1939, *Long 1154* (BOL), and cult. specimens (SRGH).

H. longii is closely related to *H. pillansii* and particularly to subspecies *echidnopsioides* but appears to be satisfactorily separated at specific level by its consistently smaller stature, more slender stems with fewer angles and smaller, spreading (not deflexed) teeth, and an inflorescence of smaller flowers with proportionally wider (usually wider than long) corolla-lobes, shorter papillae and quite different, divergent, subulate, inner corona-lobes which are very minutely papillose at the small, sometimes very slightly enlarged apex.

The habitat of this rare species is entirely different from that of its relative which occurs on Karoo shales, often in fully exposed situations. *H. longii*, on the other hand, grows on very steep, cliff-like, conglomerate slopes, closely intermin-

gled with tufted grasses among shrubs, and associated with Euphorbia polygona, Aloe striata, Crassula lycopodioides, Haworthia sp. etc.

Stems: up to \pm 8 mm diam., with 6–8 rows of tessellate tubercles, sharply sulcate between the rows and bearing small, spreading, acute teeth (modified leaves) when young.

Pedicel: 2-5 mm long.

Sepals: ovate-acuminate, 4-4,5 mm × 1,25 mm.

Corolla: campanulate, \pm 20 mm diam., creamy yellow, smooth outside, inside spotted with crimson, minutely so inside the tube; papillae columnar, up to 0,75 mm high, 0,3 mm diam., often tipped with a minute hair; tube \pm 9 mm diam., \pm 7 mm deep, smooth inside; lobes spreading deltate, 5–7 mm long and wide, often wider than long.

Corona: inner lobes subulate, 2–2,5 mm long, dorsiventrally compressed and flattened, at first convergent, becoming divergent and recurved above, very slightly enlarged at their minutely papillose apex; nectarial orifice concealed by a prominent subacute tubercle.

Pollinia: elliptic-oblong, 0,38–0,4 mm \times 0,25 .nm.

19. Huernia distincta N.E.Br., Flora Cap. **4** (1): 910 (1909).—White & Sloane, Stapelieae, ed. 2, **3:** 956 (1937).—Luckhoff, Stapelieae S. Afr.: 222 (1952).—Jacobsen, Handb. Succ. Pl. **2:** 620 (1960) et Lexicon Succ. Pl.: 273 (1974).

Type: S. Africa, Laingsburg, Matjiesfontein, Pillans 83 (BOL!; K, holo.!).

S. AFRICA. CAPE—3320 (Montagu): near Whitehill (-AA), fl. xii.1926, Archer 270 (BOL), ibid. cult. Karoo Gdn., Whitehill. fl. v.1933, Archer 630 (BOL); ± 3 km E of Matjiesfontein, cult. "Rosedale" and Kew, 1904, Pillans 83 (BOL, K); Laingsburg (-BB), cult. Karoo Gdn., Worcester, sub 391/71, Conradie s.n. (PRE). —3321 (Ladismith): "Ladismith Distr.", cult. Karoo Gdn., Worcester, sub 154/72, A. J. Joubert s.n. (PRE).

Stems: 8–9 (mostly 8)-angled, strongly reminiscent of those of *H. pillansii* subsp. *pillansii* but with more strongly toothed, fewer, more prominent angles.

Pedicel: 6-12 mm long.

Sepals: ovate-acuminate, very variable in length even in the same flower, 6–12 mm long, 1.5–2 mm wide.

Corolla: 30–36 mm diam., dull yellow, smooth outside; inside densely papillose, marked with red (''crimson'') blotches, and in the tube with broken transverse lines; papillae cylindric, obtuse, up to 1 mm high (Joubert 0,75 mm), each tipped with a stout, often subclavate, dark red or red-tipped bristle; tube campanulate, 12–14 mm diam., 11–12,5 mm long, smooth inside; lobes widely spreading, often recurved, deltate-acute, 9–10 mm long, 9–11 mm wide.

Corona: inner lobes slender, subulate, with micro-tuberculate scabrous, very slightly enlarged apices, often scabridulous down to about half their length, somewhat swollen or gibbous at their base, 3–3,5 mm long, at first convergent then diverging from about half-way; nectarial orifice obscured by a rather small tubercle.

Pollinia: oblong-elliptic, $0.38-0.4 \text{ mm} \times 0.25-0.29 \text{ mm}$.

This species was considered by N. S. Pillans probably to be a hybrid between *H. pillansii* and *H. clavigera* Haw, which both occur in the same area. However, the considerable extent of uniformity to be observed between the initial and subsequent gatherings, together with the repeated occurrence of the species, suggest that it may after all prove to be a "good" species. In any event, whatever its precise ancestry, it seems clear on the evidence of its stems and papillae that it belongs in the "pillansii" relationship, while the corona and the corolla bristles seem to indicate a similarly strong connection with *H. clavigera*.

ACKNOWLEDGEMENTS

I am most grateful to the many friends and colleagues, too numerous to be mentioned individually here, who have contributed to this study in a variety of ways, particularly with many gifts of living plants and other material.

My sincere thanks are also due to the Directors of the: Botanisches Museum, Berlin-Dahlem (B); the Bolus Herbarium, University of Cape Town (BOL); the Herbarium of the Albany Museum, Grahamstown (GRA); the Royal Botanic Gardens, Kew (K); the Centro de Botânica, Lisboa (LISC); the Botanische Staatssammlung, München (M); the National Botanic Gardens, Kirstenbosch (NBG); the Natal Herbarium, Durban (NH); the National Herbarium, Pretoria (PRE); the Herbarium, Swedish Museum of Natural History, Stockholm (S), and the Institut für Systematische Botanik, Zürich (Z), for the facilities of those herbaria which have been visited, for the loan of valuable material, for photocopies of pages from the literature and information concerning type specimens and nomenclatural matters.

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BOOK REVIEWS

FLOWERING TROPICAL CLIMBERS, by Geoffrey Herklots, with pp. 194, 270 line drawing and 16 full colour plates. (In slip case.) Folkestone, Kent: Dawson Science History Publications, 1976. £17.50.

In his preface to *Flowering Tropical Climbers*, the author states that his book "is intended primarily as a guide to students who are studying the ecology of tropical plants". This seems to me a rather misleading remark as the book is actually a systematic enumeration of some of the better known ornamental climbers cultivated in the tropics.

The species discussed are dealt with under families, the families being arranged in alphabetical order; but there are no keys to the families or genera and only in a few cases are keys to the species given. This will tend to make finding ones way around a little awkward, except for those with some knowledge of angiosperm systematics. Geoffrey Herklots, however, is one of those extraordinarily talented persons who is a master of the art of line drawing. In all, 270 of his beautifully executed line drawings illustrate the text. They are accurate, clear and diagnostic as well as being aesthetically pleasing and all have been drawn from living material studied by the author at an impressive number of exotic places in the tropics during the greater part of his lifetime. These drawings are the very core of the book and may well prove more useful than a plethora of keys. The 16 colour plates are less successful, however.

Likewise, the text is based on original observations particularly in so far as the cultural notes are concerned. In addition to a description of each species discussed, important synonyms and distribution data are given. It is very difficult to assess the completeness of this book, but in general, it would seem that the more spectacular horticultural subjects appear to have been given preference. In the final analysis the author's selection seems to have been a very personal one. One wonders, for instance, how *Clematis montana*, a Himalayan species, hardy in English gardens, came to be included in a book on tropical climbers, while *Clematis brachiata*, widely distributed in southern Africa is omitted. *Combretum microphyllum*, a splendid subtropical African species is also missing; although possibly the author considers it synonymous with the related *C. paniculatum*, which is listed.

Horticulturists working in the warmer parts of the world will find this publication an invaluable guide in the selection of suitable material. I believe it will also be useful to botanists who have to name specimens of cultivated tropical climbers without having access to adequate library facilities. But priced at £17.50 this somewhat specialized volume will be beyond the means of most, except of course affluent tax exiles on Caribbean Islands who intend to refurbish their gardens with some of the tantalizing climbers which Dr Herklots has so skilfully brought to our attention. All in all, this carefully written book will surely fill a gap in the literature as it deals with a subject which appears to have been completely ignored in the past.

J. P. ROURKE

PLANT PATHOGENESIS, by H. Wheeler, with pp. x, 106, 19 figures and 5 tables. Berlin—Heidelberg—New York: Springer-Verlag, 1975. U.S. \$16,00.

Plant Pathogenesis is a slim but sturdily bound volume of 106 pages with 19 figures (half-tones and graphs) and 5 tables.

It is the second volume of an Advanced Series in Agricultural Sciences, in which the editors set out to provide concise, up-to-date, texts for "advanced undergraduate and early

graduate students in agriculture", texts which will also be "helpful to extension specialists who have an ever-present need for the latest information in the day-to-day solving of practical problems". The author of the present volume intends it "... to serve as a text for advanced undergraduate and graduate students in plant sciences and as a reference source for students, researchers and technologists".

There are six chapters. Chapter 1 is a brief review of modern concepts of plant diseases and their causes, pathogenicity and the disease reaction. This is followed by a description of the penetration process and the "offensive weapons" employed by pathogens: enzymes, growth regulators and toxins. Chapter 3 deals with the response of plants to infection: pathological alterations in structure, function and metabolism. Those mechanisms of disease resistance not covered in previous chapters are dealt with in Chapter 4. Chapter 5 discusses genetic aspects of pathogenesis, while in the final chapter the author introduces the concept of a physiological syndrome: "a sequence of changes in pathogenesis triggered by some initial event".

Plant Pathogenesis is an advanced reference text. It is up-to-date: more than 100 of the nearly 200 references are dated 1970 or later and most of the half-tones are either transmission or scanning electron micrographs. It is well-written. The bulk of the material is factual, though Chapter 1 is concisely philosophical and Chapters 5 and 6 admittedly speculative. Particularly stimulating is the treatment of Flor's gene-for-gene hypothesis in Chapter 5.

Plant Pathogenesis will find little place in the bookshelf of the extension specialist involved in solving practical problems in the agricultural field, but in the South African context it should be compulsory reading for final year plant pathology undergraduate students, postgraduate botany students specializing in plant pathology, and university teachers in these fields. Unfortunately the price of the volume (U.S. \$16,00) is such that only the dedicated will acquire their own copies.

P. S. KNOX-DAVIES

ADVANCES IN RESEARCH AND TECHNOLOGY OF SEEDS, PART 1, edited by W. T. Bradnock. Wageningen, Centre for Agricultural Publishing and Documentation, 1975. Price Df35.

This book consists of a series of short reviews on recent advances in seed physiology and technology, and is a successor to the *Seed Bibliography* previously published at intervals by the International Seed Testing Association. It is intended to produce further issues on a range of topics concerned with seed biology as the subject advances. Only work published since 1970 is included in the reviews contained in the present issue, and in the reviewer's opinion, this is the real value of the book.

The subjects covered in this first issue are germination, a short specialist section on tree and shrub seeds, seed dormancy, seed pathology and seedling vigour. Only the review on seed dormancy gives any background information on general theory, the others assuming a familiarity with their subjects and utilizing their available space for coverage of newly-published research results. This of course rules out the possibility of use by students or newcomers to seed physiology, unless they are prepared to use a more general text initially.

The book will therefore be of most use to specialists in seed technology, who will derive greatest benefit by being brought up to date both with new results and with the present trends of investigation in subjects peripheral to their own fields of research. The value of the reviews would be considerably increased if the editor could induce writers to include comment on the results presented, and indicate areas of work which require to be extended. If the original aim of producing a continuing series of these works is achieved, a most valuable reference collection will be formed.

JOURNAL OF SOUTH AFRICAN BOTANY

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